Tussock Sedge

A Wetland Superplant

Joy Zedler

Aldo Leopold Chair of Restoration Ecology, Emerita
University of Wisconsin–Madison

Illustrated by Kandis Elliot

Senior Artist, Emerita
University of Wisconsin–Madison

ISBN 978-1-7923-8892-7
An online, science-based Book for readers in high school and beyond.

The eBook was posted online in Wisconsin, USA.

All research and researchers referred to in this Book are greatly appreciated.

The University of Wisconsin-Madison is acknowledged for its support of graduate education, especially the Aldo Leopold Chair of Restoration Ecology, held by the author and housed at the Botany Department and Arboretum from January 1998 to August 2016.

Table of Contents

Light-footed Ridgway's rail
in California salt marsh

Sandhill crane
in Wisconsin freshwater marsh

Introduction

Perhaps you are reading this because you are curious about plants. Great—this is written for you, whether you already know a lot of botany or are new to the subject. In all my years of enjoying and researching the ecology of wetlands, my inspiration has usually been plants as habitat for special birds—like a Light-footed Ridgway's rail in the salt marshes of California and the Sandhill crane in the freshwater marshes of Wisconsin. But, the more my students and I learn about Tussock sedge (*Carex stricta*), and the longer I live next to a tussock meadow, the more I am inspired by a plant that creates trunk-like structures and influences everything about the sites it occupies—its associated plants and animals, the soil conditions, and the quality of the water.

For all its many functions, I call Tussock sedge a ***"superplant".*** That's my opinion, not a technical description. However, the opinion is based on scientific studies. The purpose of this book is to share science-based information with curious readers. Luckily, Kandis Elliot (a superartist) agreed to collaborate in this venture!

Let us introduce sedges first: They are not forbs, which have broad leaves; and they are not grasses, although their long narrow leaves are easily mistaken for grass leaves. And when the sedges bloom, you might not be impressed unless you have a magnifying glass handy. Don't expect a colorful bouquet…. Of course, we enthusiasts get excited by sedge flowers because they don't have petals.

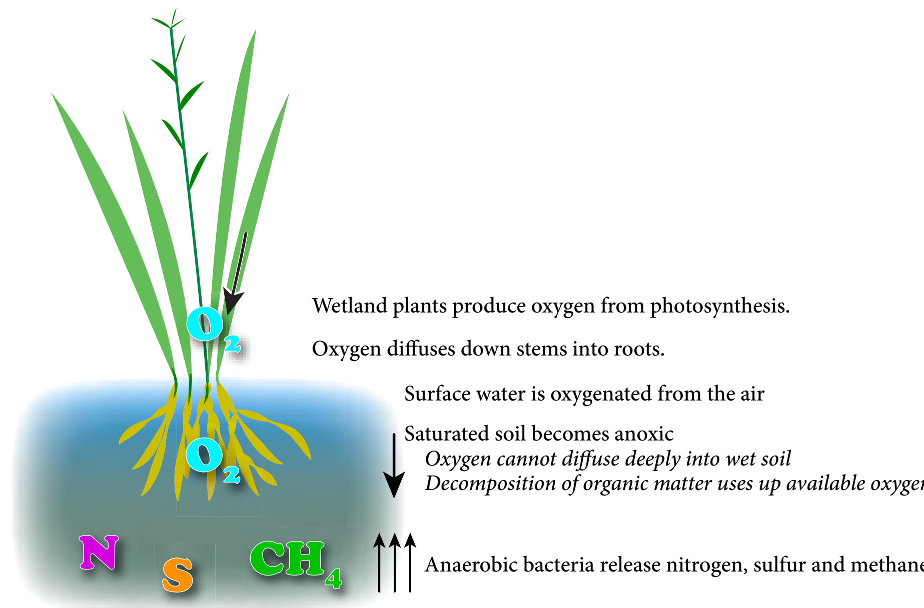
Next, we introduce wetlands. As the name indicates, "wet lands" are wetter than uplands but not as wet as oceans, lakes, and rivers. They can be hard to identify when they are temporarily dry or flooded, so we look for other clues from wetland vegetation and wetland soil. It is hard to find distinct boundaries between wetlands and uplands.

No wonder noted ecologist Eugene Odum deferred to his granddaughter, who described wetlands as "places where you step and it goes squish."

Flowers of sedges and their relatives

Grass flowers

Wetlands are far more important than their global area suggests. How do wetlands provide so many benefits in so little area? It's because wet places develop **anoxic (anaerobic) soil** (with very little or no oxygen). Wetland plants have ways to move oxygen from the air to their roots. Amazing! At the same time, the anoxic soil makes it possible for wetland bacteria to carry out chemical processes that release nitrogen, liberate sulfur, and oxidize methane. These and other processes influence the cycles of several elements that are needed by organisms, including people. Those are *facts,* not opinions.



This book features Tussock sedge, which lives in squishy places. It's about the studies that many of my UW graduate students carried out over two decades—what we learned and how we learned it. It also reports how my backyard Tussock sedge grew leaves and fruits and then senesced over eleven growing seasons. Next, the book documents nine ecosystem services that make tussock meadows highly valuable and Tussock sedge a wetland superplant. But despite extraordinary services, the sad fate of many wetlands is drainage or filling. So the book presents advice for wetland **restoration and protection.** The more technical text is in boxes, and some thought-provoking issues are highlighted in yellow. There are no quizzes, just science-based information and illustrations. Happy reading!

Creekside tussocks

Photo: J. Zedler

1
What's unique about sedges?

Sedges aren't showy plants. Most are short plants with narrow leaves. They blend in with grasses and are often overgrown by showier plants with broad leaves and colorful flowers. They might not grab your attention, but sedges are more important than they appear. The ones that live in wetlands are especially useful and worthy of attention.

Sedges are unique because of what they are and what they are not—they are **not** grasses, although their long, slender leaves do look a lot like those of many grasses. They are **not** showy forbs, even though their flowers are quite interesting up close. They are not woody plants like shrubs and trees, even though those that produce tussocks seem to have "trunks". Sedges **are** flowering plants, along with about 270,000 other species worldwide, but you'll need a hand lens to see the flowers and seeds of most sedges. They **are** herbaceous plants with long narrow leaves.

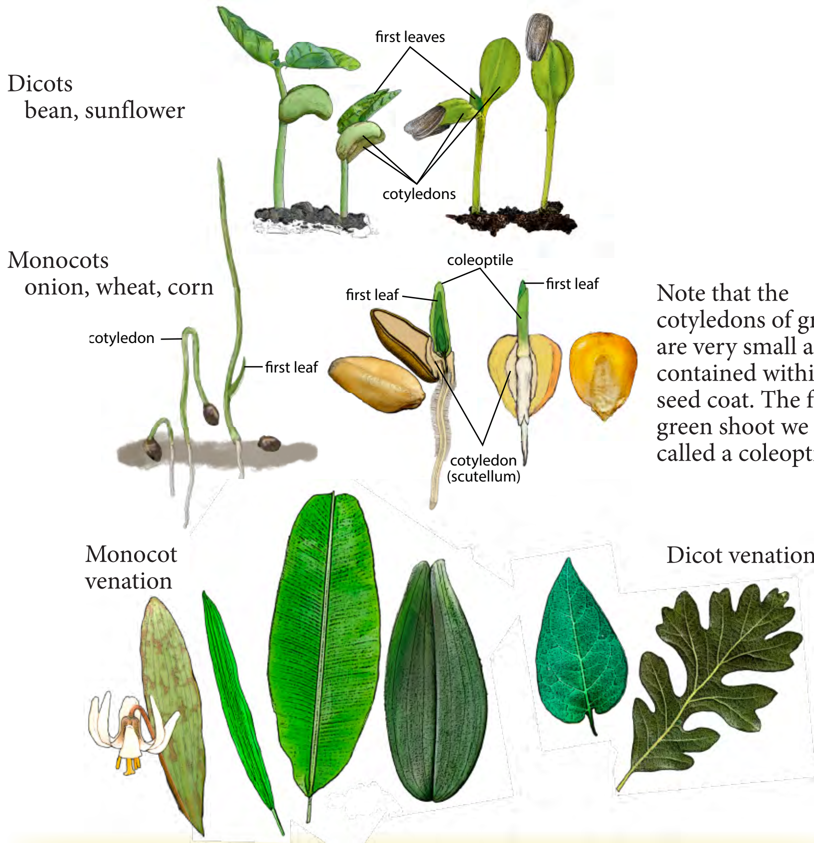
Some sedges are **annual plants** that reproduce only by seed and then die at the end of the growing season. Most sedges are **perennial plants** that live longer; their leaves die to the ground each fall, while their roots and rhizomes belowground stay dormant over winter and send up new shoots every spring. Annuals "start from scratch" (a seed) every year; perennial sedges accumulate biomass belowground over many years.

Sedges and rushes and grasses are related, but these groups of species belong to unique families: Cyperaceae, Juncaceae and Poaceae, even though they look similar from a distance. Also, they can be confused when they are not in flower or dropping seeds. They are all Monocotyledons, which you can tell when a seed germinates and produces a "mono" (single) "cotyledon" (seed leaf).

"Sedges have edges" someone said a long time ago. That's because the stems of the plant form a triangle in cross-section. Grass stems are round. These are "rules of thumb," meaning they are generally true.

Sedge stem

The world's flowering plants belong to either the Monocotyledons or Dicotyledons (nicknamed "Monocots" and "Dicots"). While their group name tells you how many seed leaves there are, each group has many more characteristics that differ. For example, Monocots have leaves with parallel veins. Included are lilies and irises. Dicots have branched veins; think of an oak leaf. There are fewer Monocots (~60,000 species) on Earth than Dicots (~175,000 species).



Note that the cotyledons of grains are very small and contained within the seed coat. The first green shoot we see is called a coleoptile.

CRITICAL THINKING • Grab a small handful of grass leaves with stems from a nearby lawn. Look closely at the veins that move water up from the soil to the leaves and move starches and sugars down from the leaves to the roots and rhizomes. Are the veins parallel? Yes. Look at the cross-section of the base of a grass stem. Is it round? Yes. If you happen to pluck a square stem, try smelling it to see if it is a mint (which is a Dicot, although most Dicots have round stems).

CRITICAL THINKING • Which Monocots play important roles in the human diet? Did you eat anything this week that did not include at least one Monocot? Or if you ate meat, did the animal's food include Monocots? Hint: We eat a lot of grass seeds, especially corn, wheat, rice and barley, plus oats, millet, sorghum, and wild rice. You can probably germinate a few raw seeds by keeping them moist in a clear container in daylight. Once they germinate, you'll have evidence that they are Monocots. Other Monocots that we eat would not be so easy to grow, e.g., coconuts, sugarcane, palm oil, bananas, pineapples, asparagus, onions, shallots and garlic. Grass seeds have been gathered and cultivated by humans for millennia. Seeds are easily transported, ground to make bread, or stored for later use.

One edible member of the sedge family (Cyperaceae) is a favorite crunchy ingredient in Asian stir-fry recipes. Water chestnut (*Eleocharis dulces*) has a delicious corm (bulb-like storage organ) that is grown commercially with a complicated hydroperiod. *Eleocharis* and *Carex* are genera (plural of genus) in the same family.

In addition to the genus *Carex*, the family Cyperaceae has about 90 other genera. Globally, **the genus *Carex* has about 2,000 species.** Of these, 157 species of *Carex* occur in Wisconsin, according to Andrew Hipp, whose book is a "must have" for Wisconsin botanists!

Sedge flowers and fruits differ a lot from those of all other plant families, and they differ a little from each other. Taxonomists inspect the plants, especially the flowers and fruits, to sort them into species. Nowadays they use DNA to identify close vs. distant relatives. Each member of a species can breed with other members, and their offspring resemble their parents.

The plant that was used to make paper in ancient times (as early as 2555 BC) is a member of the Cyperaceae (Papyrus = *Cyperus papyrus*). Stems were peeled and the inner pith was aligned in long strips and press-dried, and later polished, to make smooth sheets. Although native to the lower Nile River, this species is now extinct in Egypt.

Papyrus stem

Sometimes members of different species interbreed and produce hybrids. That's often the case with cattails (another Monocot, this one in the Genus *Typha,* family Typhaceae). What's important to know about hybrids is that some are very aggressive plants ("hybrid vigor"). *Typha* x *glauca* is an aggressive, invasive hybrid between the native *T. latifiolia* and the introduced *T. angustifolia* (from Eurasia).

T. latifolia • Broad-leafed cattail

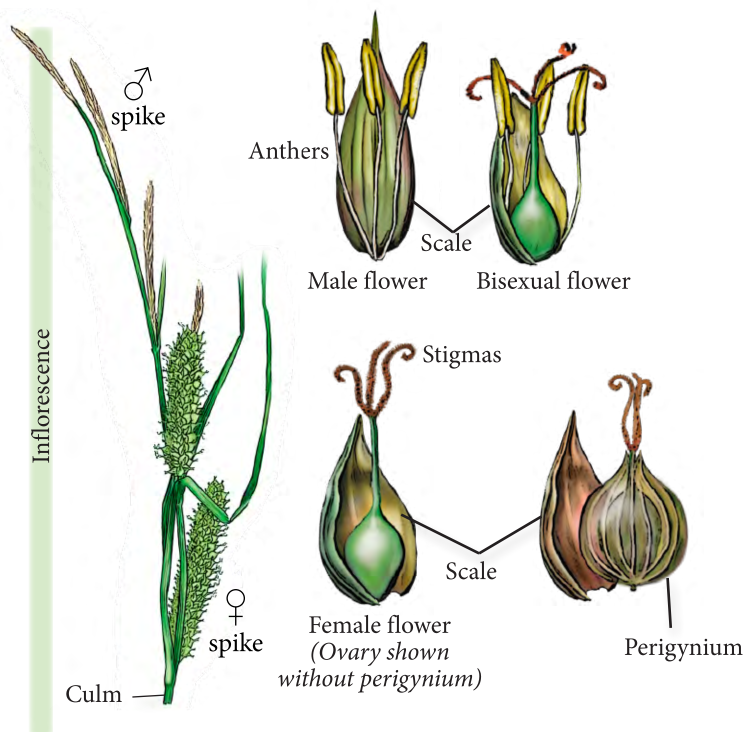
T. angustifolia • Narrow-leaved cattail (note gap between male and female inflorescences)

Carex grayi is a Wisconsin sedge with perigynia arranged in a spikey ball, like a medieval flail. A flail is large and made of heavy metal, whereas the sedge fruit is only 2–3 cm in diameter and light in weight.

Sedge flowers have no petals. The **male flowers** produce pollen, which fertilizes the female flowers. Male flowers grow in a group (spike = a set of flowers with a scale at their base) that forms an **inflorescence** at the tip of a stem **(culm)**.

The **female flowers** also grow in inflorescences, usually made up of several spikes. Each female flower has a tiny vase-like **perigynium** (a structure "around the flower parts") that produces each fruit. The sticky **stigmas** are usually fork-like with 2 or 3 "tongs" that poke out of the perigynium and collect pollen that falls from or is blown from male flowers.

CRITICAL THINKING • Why are the male flowers usually produced above the female flowers? Tall culms make sense for male flowers because: The wind can easily blow the pollen when the male flowers are above the leaf canopy. Pollen produced high in the canopy can fall onto the female flowers.



Sedge fruits • The most important work that a sedge (and any other plant) can do is to reproduce. In *Carex stricta,* this happens very early in spring. It begins with pollen encountering the **stigma.** Once attached to the stigma, a pollen grain can grow toward the ovary and form a seed (plus seed wall = a one-seeded **achene**). Some achenes are shaped like a lens; some are 3-sided. The perigynium and achenes have unique features that help us identify the species.

Ripe sedge fruit

Sedge seeds • They are tiny, of course, but since they grow in inflorescences with many flowers, the group of flowers is easier to see. You can find them and shake the seeds onto your hand or the ground.

Vegetative reproduction • Many sedges reproduce vegetatively by growing new shoots from underground stems **(rhizomes).** Often, the rhizomes are long with widely-spaced nodes (growing points); this separates the shoots and allows rapid expansion of the resulting clone. Some plants have short rhizomes and form tight clusters

or clumps (**cespitose** form). *Carex pensylvanica* is a common woodland sedge that is usually cespitose. *Carex stricta* can grow both short and long rhizomes.

Carex barbarae, known as White root, forms large clones in valley oak woodlands in California. Native Americans used the long rhizomes of this vegetatively reproducing sedge to weave baskets for a variety of uses. Tending (weeding and planting) was needed to sustain harvesting every 2–4 years. These Traditional Resource Management practices greatly influenced the understories of riparian woodlands.


C. pensylvanica inflorescence and clumped growth habit

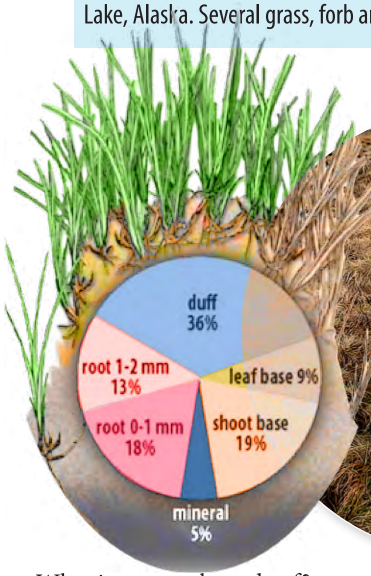

White root sedge basket
Photo courtesy of: M. Stevens

CRITICAL THINKING • ***Review key features:*** Sedges (Cyperaceae family) are herbaceous Monocots with tiny flowers without petals. Male flowers form inflorescences at the tip of the canopy; female flowers catch pollen that falls or blows in the wind. Their leaves have parallel veins and are usually narrow. Sedge stems are usually triangular in cross section; "sedges have edges."

2
Is there a special wetland sedge?

Which species of *Carex* deserves an entire book about its feats? In my opinion, it is **Tussock sedge** (*Carex stricta*). This book explains why it's special and how my students at the University of Wisconsin–Madison and other researchers have learned about the many important things that this species does for Nature and for people. As we will show in Chapter 3, Tussock sedge grows fast, spreads vegetatively, and forms tall tussocks that enhance bumpiness (topographic heterogeneity), support dozens of other plant species, sequester carbon, soak up water, remove nitrogen and phosphorus from nutrient-rich runoff, aerate the root zone (rhizosphere), and create habitat for small mammals.

What are tussocks? They are upright clusters of **leaf and shoot bases** (28%), **roots** (31%), and **duff** (36% decomposing debris) and some mineral material. Tussocks grow slowly but reach heights of 0.3–0.6 m in wetter soil. Tussock sedge also expands laterally (over the soil) by growing rhizomes that spread under the soil surface (as much as 0.5 m/year). Tussocks are especially visible in winter, after the canopy of leaves has collapsed, leaving a landscape of bumps (microtopography). Other well-studied tussocks dominate tussock tundra at Toolik Lake, Alaska. Several grass, forb and woody species form the tussocks.




Bumpy tundra tussocks

What is a tussock made of?

Tussock sedge is a "superplant" for providing ecosystem services and for use in restoring wet meadows. I define **superplant** as *a species that provides many functions, and high levels of several functions.* As for the other ~1,999 sedge species around the world, I'm not sure what makes each one special, but I'm hoping future researchers will take up the challenge of finding out.

Threats • Despite many strong attributes, Tussock sedge meadows are vulnerable to invasion by both Reed canary grass *(Phalaris arundinacea)* and hybrid Cattails *(Typha x glauca)*. These aggressive invaders outgrow Tussock sedge in nutrient-rich conditions. In the UW Arboretum's Gardner Marsh, for example, Cattails responded to nitrogen and phosphorus (N + P) addition by growing taller and denser, keeping Tussock sedge from capturing enough nutrients and light to compete with the invader. Both Reed canary grass and hybrid Cattails require aggressive management and continual surveillance—before, during and after tussock meadow restoration.


Reed canary grass stand


Hybrid cattails

Where have all the sedges gone? A lot of sedges haven't gone anywhere. Various species still live in the country's wetlands and uplands, near open water and in woodlands. Tussock sedge can thrive in low-nutrient wetlands. It doesn't process nitrogen as well as aggressive invasive grasses or hybrid cattails, so we can look for Tussock sedge in wetlands that have escaped the combined disturbances of cultivation, urbanization, and groundwater depletion. Tussock sedge is still the *matrix species* in sedge meadows throughout the Upper Midwestern and Northeastern USA, including Great Lakes coastal wetlands. By saying "matrix," doctoral student Christin Frieswyk emphasized the ability of Tussock sedge to be abundant and also create habitat for other species, not displacing them.

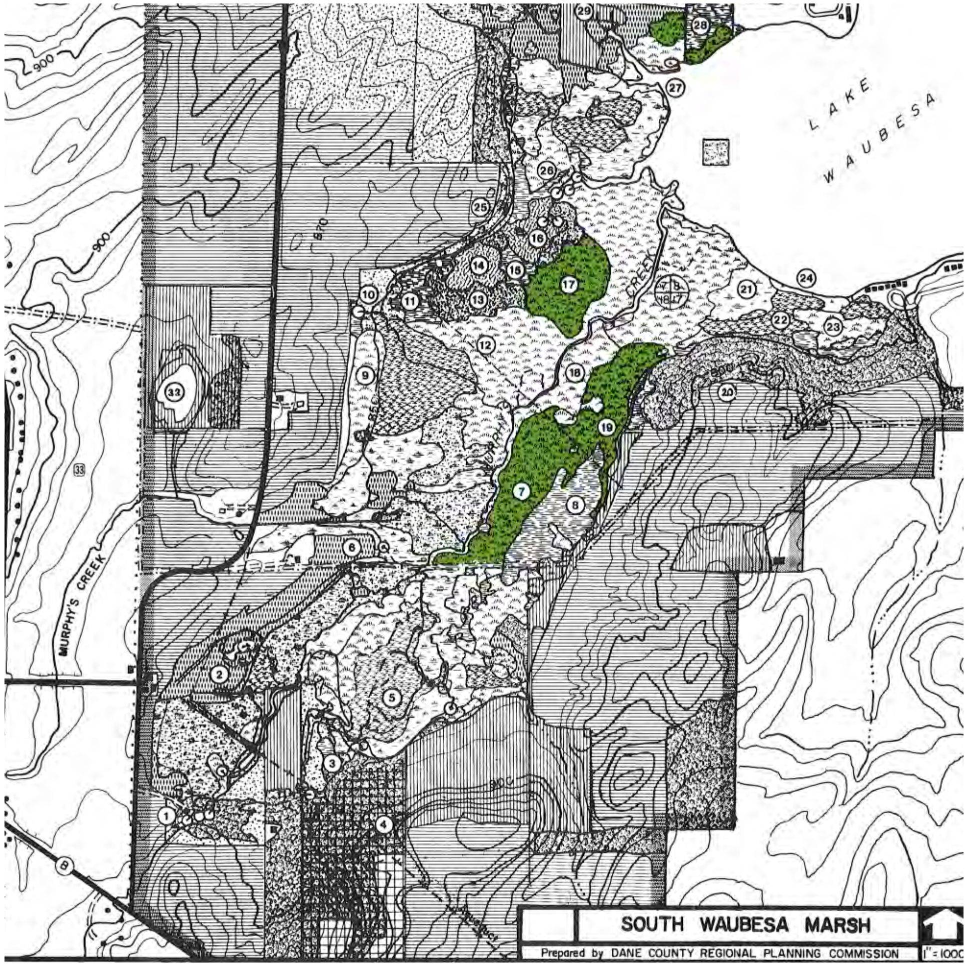
Where should we look for *Carex stricta?* First, we need to find wet places that have saturated soil in spring, followed by a water-level drawdown in late summer. That water-level pattern is Tussock sedge's preferred **hydroperiod.** Often the water source is groundwater that rises to the surface via seepages and springs. Compared to surface-water runoff, groundwater is usually has fewer nutrients. In contrast, surface water flows across the land, where it picks up nutrients and moves nitrogen and phosphorus towards the low spots in the landscape.

In short, **we should look for Tussock sedge in Nature reserves.** Many former sedge meadows near Madison, Wisconsin, lost their critical water supply when wetlands were drained for cultivation and depleted by groundwater pumping for drinking water. Conservation reserves protect extensive sedge meadow remnants at Cherokee Marsh, Pheasant Branch Conservancy, and Waubesa Wetlands.

Wetlands on the southern shore of Lake Waubesa

Waubesa Wetlands are much appreciated by residents of the Town of Dunn. They were described by Alex Wenthe, expert field ecologist, as follows: "Most the wetlands area is southern sedge meadow, dominated by lake, tussock, and sawgrass sedge (*Carex lacustris, Carex stricta, Cladium mariscus*). Rare wetland types like calcareous fen, floating sedge mat, and wet prairie also exist throughout the wetland complex. The largest fen mound, aptly named 'the great fen', contains remnant indicator species like Lesser fringed gentian (*Gentianopsis procera*), Grass of Parnassus (*Parnassia palustris*), and Kalm's lobelia (*Lobelia kalmii*). Areas of floating sedge mat and wet prairie are also floristically diverse with many conservative forb, reed, and rush species.

Statewide, botanist Andrew Hipp described Tussock sedge as "Common in calcareous prairies, sedge meadows, fens, and peaty soils overlying wet sands primarily in the southeastern, central, and northeastern portions of the state, occasional near Lake Superior and in the Driftless Area."



In 1974, Waubesa Wetlands' sedge meadows were described by Barb Bedford and Jim Zimmerman, who walked back and forth across the wetlands and matched what they saw on the ground with what they could interpret on aerial photos. What a marvelous effort! Their map and description of the vegetation are valuable historical documents.

SOUTH WAUBESA MARSH

MAP KEY

Deep-water emergents, usually cattail, in deep water most of the year.

Various emergents, such as bur reed, cattail, C. comosa, C. lacustris, in a few inches or more of water, but not in deep water.

Mixed wetland vegetation with few or no forbs; sedges, bulrushes, scattered cattail, bluejoint, and giant reed grass (Phragmites communis). Water depth is a few inches at most.

Mixed shallow wetland vegetation with forbs, notably aster and goldenrod, usually on wet soil.

Sedges and bluejoint grasses strongly or entirely dominant.

Sedge meadow with forbs. Tussock sedge and bluejoint locally dominant, some Carex aquatilis, goldenrods, asters, scattered shrubs, cattails, and marsh dock.

Grazed sedge meadow.

Fen.

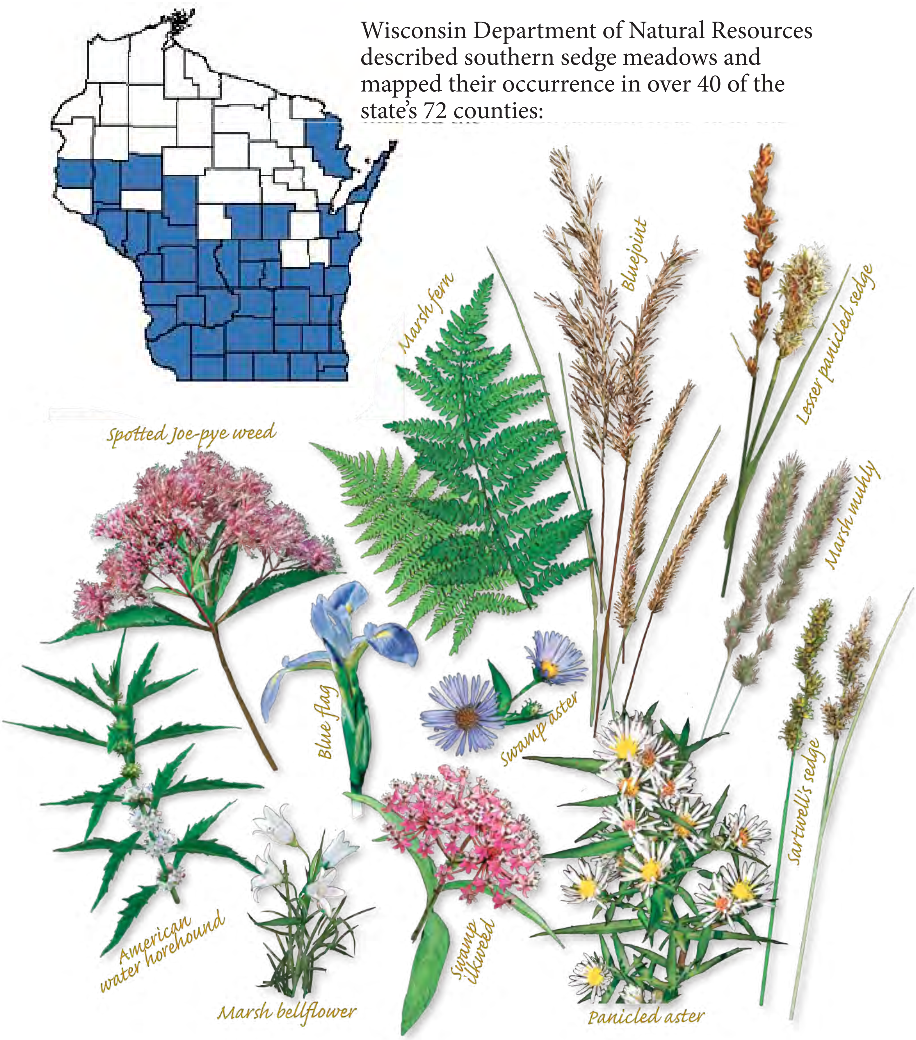
Bog birch on fen.

Lowland shrubs (mostly willows and red-osier dogwood, except as noted).

Disturbed wetland (mostly reed canary, but also other disturbance indicators).

For a map of North American sedge meadow distribution, go to Plants.USDA.gov (https://plants.usda.gov/home/plantProfile?symbol=CAST8). Tussock sedge is called "upright sedge" in the USDA (US Department of Agriculture) database. The map shows it occurring in the eastern half of the US and Canada, including Wyoming but not Oklahoma and Florida, Labrador or Newfoundland. It's a very widespread sedge!

Southern sedge meadows are widespread in southern Wisconsin. This open wetland community is most typically dominated by Tussock sedge (*Carex stricta*) and Bluejoint grass (*Calamagrostis canadensis*). Common associates in relatively undisturbed sedge meadows are other sedges (e.g., *Carex diandra, C. sartwellii*), forbs (e.g,. Marsh bellflower, *Campanula aparinoides*), American water horehound (*Lycopus americanus*), Panicled aster (*Symphyotrichum lanceolatum*), Swamp aster (*Symphyotrichum puniceum*), Iris (*Iris* spp.), Spotted Joe-Pye weed (*Eutrochium maculatum*), Swamp milkweed (A*sclepias incarnata*), a fern, and a grass, Marsh muhly (*Muhlenbergia glomerata*). Reed canary grass *(Phalaris arundinacea*) is often dominant in grazed and ditched stands.



Wisconsin Department of Natural Resources described southern sedge meadows and mapped their occurrence in over 40 of the state's 72 counties:

3
How does Tussock sedge grow year after year?

Except for a few entirely parasitic species, like Indian pipe (*Monotropa uniflora*), all the plants around us have **chlorophyll.** That green pigment absorbs the energy from sunlight so the plant can carry out **photosynthesis,** which is the formation of organic matter from carbon dioxide and water, releasing oxygen as a by-product. Although all green plants produce organic matter and release oxygen, each species has some unique features that use environmental resources (water, nutrients, light) in its own way. Each species grows at its own times, places, and rates, and with structures (varied roots, stems, leaves) and functions that have evolved over millennia that allowed it to occur where it does. That includes various interactions with soil microbes and varied ability to repel herbivores or resprout after being damaged. Tussock sedge needs sunlight over a growing season that lasts from early spring through fall. So when does it grow the fastest and how does it persist when other native species overtop it?

When I moved next door to a sedge meadow, I could watch Tussock sedge start to grow early in the springtime, and then flower and fruit before most of the grasses and forbs (flowering plants other than grasses) were awake after their long winter dormancy. I wondered about the pattern, so I started collecting data to quantify its **phenology** (timing of plant growth and reproduction). I didn't intend to start an 11-year study, but 2005 led to 2006…and before I knew it, a decade had passed. Among other things, I realized how dynamic tussock-meadow structure is, and I learned that tall tussocks have competitive advantages. Here's how a few measurements every week turned into a long-term analysis of Tussock sedge phenology in south central Wisconsin:

What does one measure? Every study depends on the data one gathers—and ecologists can never measure everything. We make choices based on previous studies and on logistics, including time and

Tussocks by the stream.
Photos: J. Zedler

money. Because I live next to a sedge meadow, I picked a small (~0.1 ha) area next to a cold spring-fed creek, where tussocks are large and numerous. The creek is shallow and ~4 m wide, with a constant temperature (54° F). Every year the flow and the temperature are the same, because the spring is fed by groundwater that emerges a short distance upstream. The soil supporting the tussocks is saturated by additional groundwater seepage. The site never floods and never dries out.

I made an 8-meter-long path through the seepage area by laying 5 short planks (end to end) over the soil to reduce footprint damage. I could reach 14 *Carex stricta* tussocks while standing on the planks. I measured the heights of their tussocks first and then measured the leaves and flowering stalks. Because there were dozens of leaves per tussock, I decided to measure only the maximum leaf length (MLL) on each tussock by stretching the handful of leaves to reveal the longest one. I counted the number of inflorescences when present,

then measured canopy height (distance from the tussock top to the curved leaf mass). I visited the site nearly every Sunday during 11 growing seasons (late April 2005 through early November 2015).

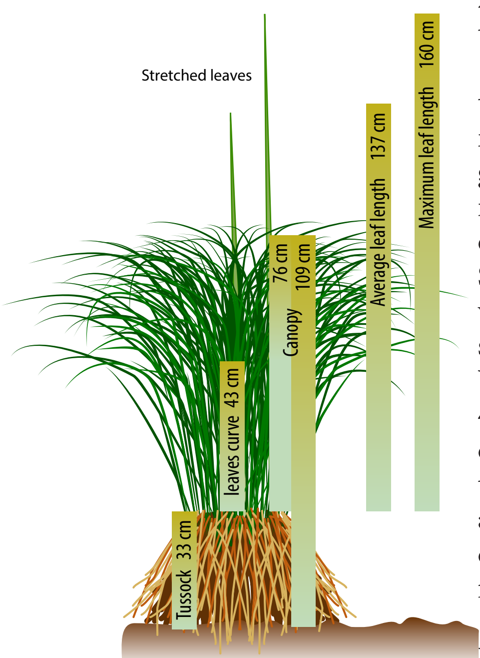
Damaged Tussock
Photo: J. Zedler

After 11 years, it was obvious that my weekly visits were damaging the soft organic soil and that deer were attracted to follow suit. It was time to summarize the data and describe **annual patterns** and long-term **trends.** In all, I had data for 294 Sundays, with over 4,000 measures of MLL and canopy height, plus counts of inflorescences in May–June. Here's how 14 tussocks and their canopies grew and flowered. I don't think anyone else has monitored sedge phenology, so my **conclusions** should be tested in other sedge meadows to see if the patterns I documented can be generalized beyond my sample site to a region. For the present, I'll just call them **findings.**

Tussock growth • The 14 *Carex stricta* tussocks followed consistent seasonal patterns, but not all tussocks survived all 11 years—more about that below. How tall were they? In 2005 the 14 tussocks (measuring soil to tussock top) averaged 33 cm. Seven years later, however, the average was shorter (22 cm). How could that be? The average remained short in 2015 (21 cm). Not only that, two tussocks near my path were unlocatable in 2015—knocked over, trampled, and flattened. The effects of monitoring were consistent with observed disturbances that included trampling and bedding by deer that followed my path. In contrast, herbivory was not obvious on the leaves. The sedge seemed to resist grazers and insects. **Finding:** Tussock sedge resists herbivory but is vulnerable to trampling.

I was surprised that the **tussocks did not grow measurably taller** over 11 tears. Part of the reason was that the ground elevation was lower where my footsteps compressed the soil, and higher where mosses and plant litter accumulated. And at the tussock top, the dense leaves made it hard to decide what the top actually was. With potential measurement errors, a small difference over time might not be real. What seemed more important than high precision was the overall pattern that 6 of the tussocks were taller than average and 8 were shorter. I noted that *C. stricta* tussocks studied by researcher David Costello in 1936 also did not show any height growth over 6 years of monitoring. **Finding:** Mature tussocks grow so slowly that it's hard to measure changes in a decade.

Annual leaf growth • When did leaves begin to grow? Tussock tops produce short, sharp shoots at the end of one growing season, in anticipation of the next. I called them "spikes." Tussock spikes were 1–3 cm tall on November 9, 2014. They overwintered and resumed growth early in spring. They grew into young leaves slowly for the first 6–7 weeks when nights were still cold. But that changed in May, when maximum leaf length (MLL) reached about 25 cm. At that point, they began elongating an average of ~15 cm/week. Wow! They reached their MLL (grand average 137 cm) near the summer solstice.



Tussock leaf growth

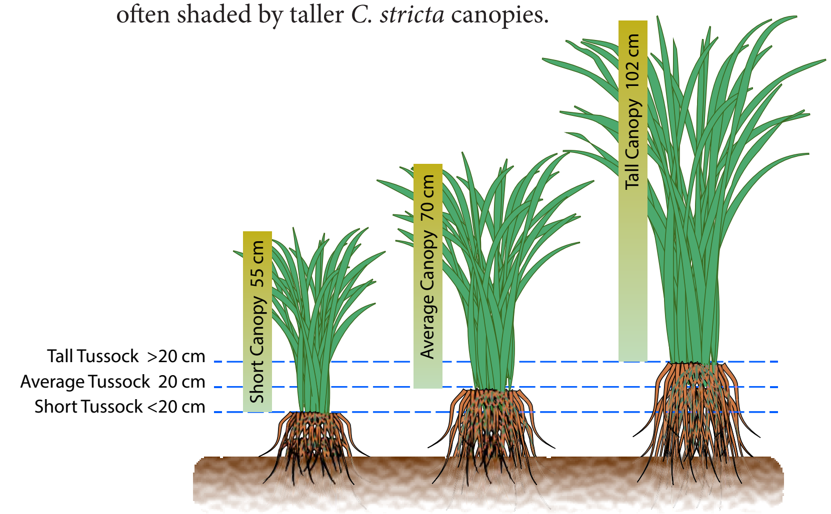
In the warm summer of 2012, four tussocks grew leaves that exceeded 140 cm by July 1, and they continued to grow to a record 160 cm! Who says monitoring is dull? Increased growth under high temperature is consistent with the findings of Texas plant physiologists Dr. Scott Holaday and students, who were growing Tussock sedge from some of my Wisconsin seeds. When leaves grew longer than 43 cm, they curved and formed a canopy that was 64–77 cm above tussock tops from June 9–24. So a 33 cm tall tussock plus its 43 cm leaf canopy measured 109 cm from the ground to canopy top.

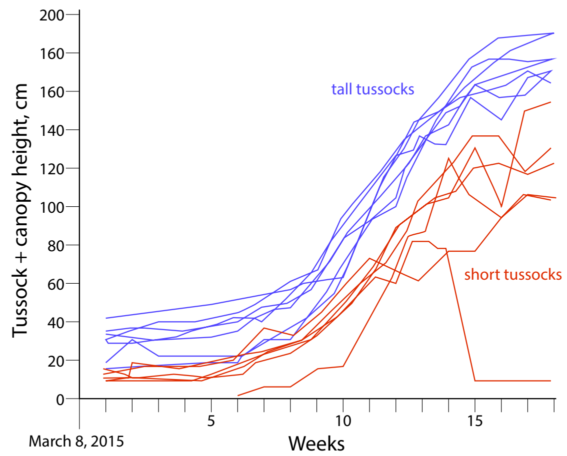
From mid-May to early November, the canopy leaves gradually senesced (slowly died), yellowing from leaf tips to bases. What did the tussocks do in winter? They were dormant (alive but inactive). Dead leaves remained attached to tussocks and persisted through the next growing season. Several tussocks were damaged by deer, which I observed in "my" 14 tussocks on February 7, 2016. Also, deer hoofprints were obvious in the snow along my path. **Finding:** Leaf elongation is slow, then linear (15 cm/week), then slow; and maximum length varies from year to year.

Flowering • The 14 monitored tussocks flowered in late April–May, with seed release in June. From 2005 through 2015, tussocks that flowered produced an average of 9.6 inflorescences. Flowering occurred in all 11 years, and 13 of the 14 tussocks flowered at least once. I counted 712 inflorescences for 14 tussocks over those 11 years. On average, a tussock flowered 5.3 times, with an average of 9.6 inflorescences per flowering event. The most inflorescences on a single tussock was 38 in 2008. Frequency of flowering and numbers of inflorescence varied together, but reproduction was not nearly as predictable as leaf elongation. **Finding:** Tall tussocks tend to produce more inflorescences (and seeds) than short tussocks, and they reproduce more often.

It pays to be tall • Average tussock height in 2015 was ~20 cm, so I divided tussocks into taller and shorter than average, and I discovered several advantages of being tall. On average, the tall tussocks produced **longer leaves and taller canopies** (height above tussocks). These results support a light-limitation hypothesis:

> Leaves higher in the canopy can absorb light first and produce more biomass. Leaves of the shortest plants were often shaded by taller *C. stricta* canopies.





In 2015, tall tussocks + tall canopies (average = 102 cm) were nearly twice the height of the short tussocks + short canopies (average = 55 cm). Growth curves for individual tussocks show that taller tussocks tended to maintain their height advantage. Another important advantage of being tall was greater reproduction! As noted above, the tall tussocks produced more inflorescences and flowered more often than short tussocks. A tall tussock could **facilitate wind pollination and long-range seed dispersal.** Other advantages were greater biomass production, ability to shade subordinates, and resistance to trampling. Not surprisingly, the **tall tussocks persisted for 11 years** of study, while the short tussocks and their canopies were victims of trampling and wildlife damage, such as deer bedding. **Finding:** Tall tussocks provide a huge advantage by elevating the aboveground biomass high in the canopy, where the leaves can capture more light and the seeds can (likely) disperse further. Tall tussocks also seem to be less vulnerable to trampling by deer.

CRITICAL THINKING • Consider the adaptive value of the tussock growth form. If tussocks are so terrific and convey such advantages, why don't more species produce tussocks? Why don't *Carex stricta* tussocks grow tall faster? Can you think of any disadvantages? How about trade-offs? If a tussock gets too tall, do roots and rhizomes near the top risk drought? Might there be an optimal rate of height growth per resource uptake and transfer from belowground? More research is needed!

Lessons about monitoring • Regrettably, I changed the ecosystem by trying to measure its plants. With the advantage of hindsight, any future monitoring could be improved with a few guidelines:

1 • *Minimize trampling in tussock meadows.* Weekly walking compressed the organic soil, appeared to slow tussock growth, and encouraged wildlife to use the same path and bed down on top of shorter tussocks.

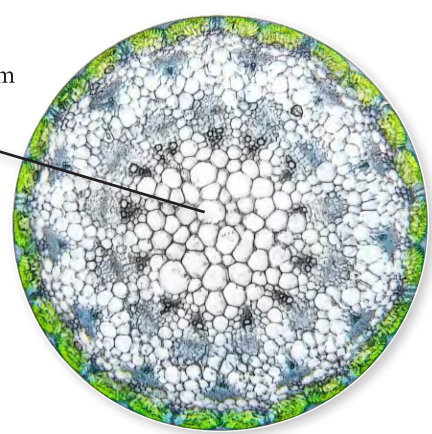
2 • *Conduct further research* to quantify the effects of direct and indirect human impacts (i.e., trampling and creating paths).

3 • *Sample less often.* Critical times are mid-May (to measure early leaf length and to count inflorescences) and in mid-June (for late leaf length, to calculate a monthly elongation rate).

4
What makes Tussock sedge a Superplant?

Tussock sedge plants create structures that do more than make the surface of the land bumpy. Their tussocks have many "talents" that benefit people. Ecologists call these useful functions **ecosystem services.** This chapter lists nine ecosystem services that tussock meadows provide for our use! There are more if we consider social values like personal enjoyment, but the nine that I feature are widely agreed-upon. The number-one service listed below is **diversity support.** This service is easy to see and to appreciate, and we illustrate many of the plants and animals that need wetlands in order to grow and nest and reproduce.

Other functions are not so obvious. An example is **nitrogen removal.** Nobody can see it happen, even though it occurs in wetlands around the globe. Why is that? It's because wetland plants and microbes (especially bacteria) create two kinds of micro-environments—*aerobic* (with oxygen) and *anaerobic* (without). The microbes thrive in moist soil and quickly use up the oxygen, making the wetland soil anaerobic and suitable for anaerobic bacteria, such as nitrogen removers (*denitrifiers*). Meanwhile, the plants that can grow in wetlands send their air-filled roots and below-ground stems into the soil. Their air-filled tissues, called **aerenchyma**, allow oxygen to flow from the leaves into the roots, which need oxygen to survive. Some of the oxygen leaks from the roots into the anaerobic soil. The close proximity of aerobic soil around roots and anaerobic soil promotes the extraordinary service of nitrogen removal. This service involves bacteria that need aerobic soil (thanks to plant roots) and others that need anaerobic soil. Together, they remove nitrogen from the soil!



What does that have to do with tussocks? Below, I estimate that tussocks can add 40% more surface area across a square meter of wetland than a flat surface. With more surface area (and more *anaerobic + aerobic microenvironments*), the tussock meadow can **remove more nitrogen**. Without wetlands, excess nitrogen would likely flow off the uplands, polluting streams, rivers, lakes, and near-shore ocean waters. Sadly, that happens where too few wetlands remain in our watersheds, and the downstream result is algal blooms (sometimes toxic) and lakes where it's not safe to swim. Where the water is clean and clear, there's likely an ample supply of wetlands upstream!

The take-home message: A basic difference between wetlands and other ecosystems (i.e., uplands and deep waters) is that wetlands have anaerobic environments with aerobic micro-sites that allow anaerobic and aerobic microbes to carry out the chemical reactions involved in nitrogen removal..

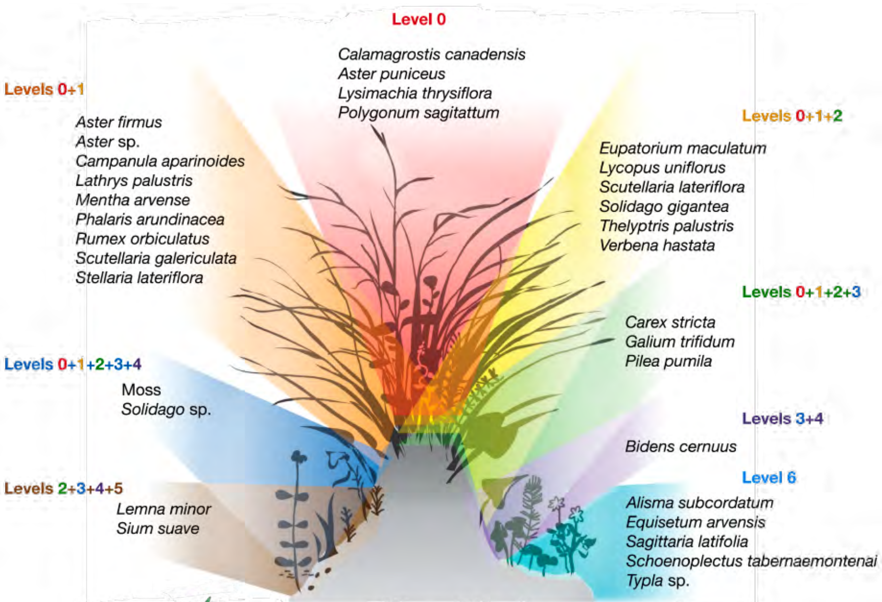
Tussock meadows provide at least nine ecosystem services, making Tussock sedge a SUPERPLANT in my book. Literally.

First Ecosystem Service • Tussock sedge supports species diversity. Why do some wetlands support more plant species than others? One way is to grow tussocks. In Wisconsin, a single tussock can support at least 16 other plant species, and a meadow with complex microtopography can support 2–3 dozen native plant species, as summarized in the table below, from former students' work.

Table 1
Species richness of *Carex stricta* tussocks in Dane County, WI

Sites	1	2	3	4	5	6
Number of tussocks sampled	15	15	15	82	121	88
Mean tussock height	6.0	17	11	15.8	14.3	27.7
Standard error (cm)	0.01	0.1	0.1	0.86	0.75	3.05
Total number of species	12	24	28	19	19	34

In Great Lakes sedge meadows, a study led by Dr. Carol Johnston found that tussocks averaged 19 cm tall. Our doctoral student Christin Frieswyk dubbed *Carex stricta* a **matrix dominant** because it shared space and allowed other species to co-exist. Christin made history by developing a clear definition of "dominance" and



Spatial segregation

Nine common species that grow on *Carex stricta* tussocks: Northern bugleweed (*Lycopus uniflorus*), *Duckweed (Lemna minor), Clearweed (Pilea pumila), Fragrant bedstraw (Galium trifolium), Blue Skullcap (Scutelaria lateriflora), Swamp aster (Symphyotrichum puniceum),* Shining Aster (*Symphyotrichum firmus*) Horsetail (*Equisetum arvense*), *Wild mint (Mentha arvensis).*

a quantitative index to compare species, using just three attributes: species that scored **high in cover** (a measure of abundance), **suppressed other spec**ies (shared 1-m^2 plots with few species), and tended toward **high cover** (likely to be abundant when present).

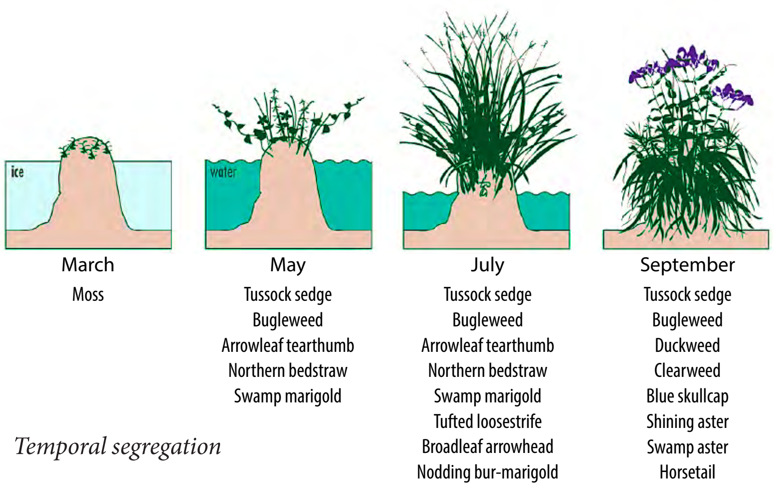
Only 38 species recorded in 74 randomly selected Great Lakes wetlands met our definition of **"dominant."** I had expected many more, given that there was a total of 466 species in the 74 wetlands. That shows why it's important to use objective criteria to characterize dominants. Thanks to Christin's objective index, we learned that most species did not become dominant. Half of the 38 species were **monotype dominants,** scoring high in all three attributes. Fewer species were **matrix dominants,** which *did not suppress* others. Hmmm: These almost seem like human attributes—some can share and cooperate, while others are always bullies. Guess how Cattails dominate: You're correct; they tend to form monotypes.

How do matrix dominants co-exist with other species? If the various plant species need the same resources (light, water, nutrients), why don't they compete till one outgrows all the others? Two reasons are that there is *spatial separation* (so they use the same resources but from different places) and temporal segregation (using the same resources but at different times).

Spatial segregation among sedge-meadow plants means that they tend to thrive in different places—for example, growing better on tussock tops than on sides or between tussocks. For example, Michelle Peach found more water-tolerant species at the bases of tussocks and more drought tolerant species on tussock tops. Also, tussock tops allow more species to grow than flat inter-tussock spaces. If each species has a preferred niche, and each tussock provides several niches, then several species should be able to co-exist. In a former "mitigation site" (a gravel pit converted to a wetland to make up for damages to wetlands elsewhere), diverse vegetation was attributed to beaver activity, tussocks, and salvaged seed. Over 35 years, the substrate became more heterogeneous, with more diversity promoting more diversity (a feedback mechanism).

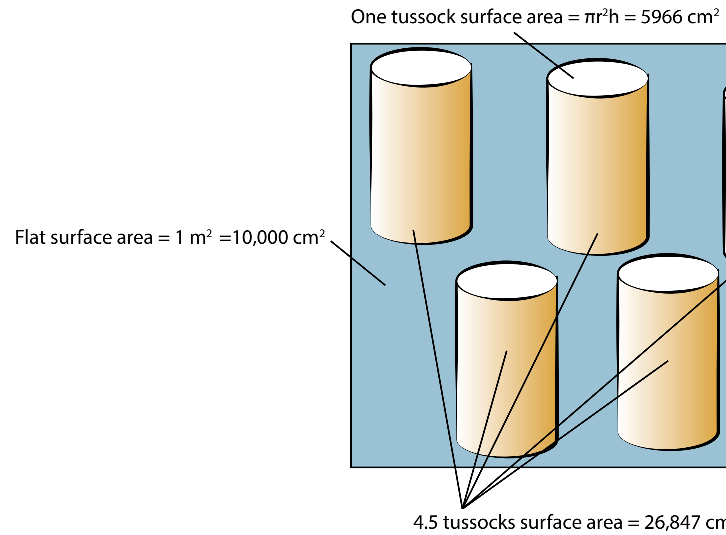
Temporal segregation seems obvious in Wisconsin tussock meadows, with sedges beating most forbs to the punch. This is easy to see. Just watch several tussocks over four seasons. In winter, you'll see diverse mosses and liverworts. In spring, the sedge leaves grow to form a canopy that shifts toward forbs in summer. And in autumn, forbs become dominant. The *Carex stricta* canopy expands to ~100% cover by the end of June, but "understory" species can still germinate and grow where there are canopy gaps. Such gaps might form when animals or winds create openings. A diversity of plants can co-exist by using light, nutrients, and canopy space at different times.

Tussock sedge spring growth

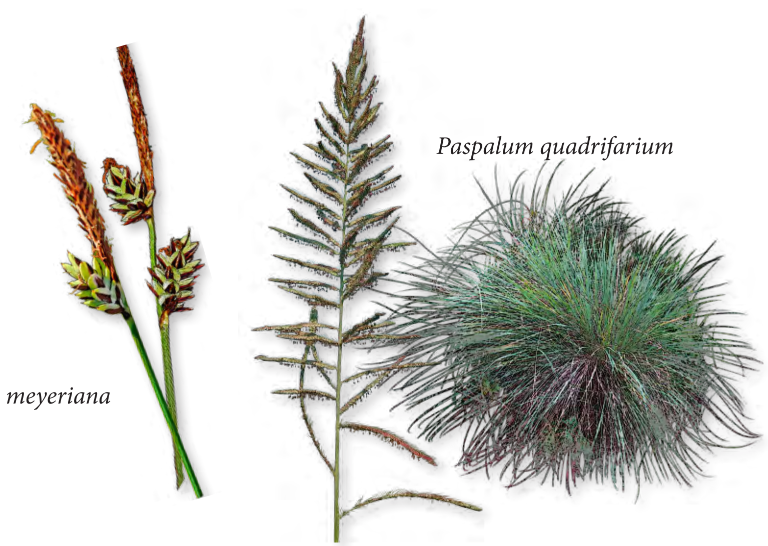


Temporal segregation

There is widespread evidence that larger tussocks, which have more surface area, can support more species. Field studies by graduate students Katy Werner and Michelle Peach found that tall tussocks support more species than short ones. Similarly, in China, Ming Wang and collaborators found that the larger tussocks of *Carex meyeriana* support more species than smaller tussocks (with size measured as basal area, height and surface area). And in Argentina's Flooding Pampa grasslands, the native tussock-forming grass *Paspalum quadrifarium* supports a higher diversity of plant species than where grass tussocks are absent—suggesting a cause-effect relationship to researcher Perelman and co-authors.



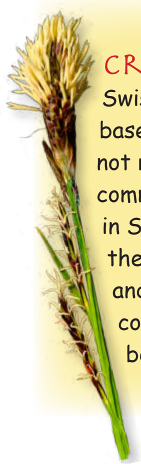
The effect of area • Does diversity increase because a mound adds surface area? Perhaps. . . . Let's see how much area a mound adds by calculating the difference in total surface area between a flat square meter (= 1 m^2) and a square meter with 4.5 mounds, as in a tussock meadow. If we assume that a mound is a cylinder, the side-surface area would = $\pi r^2 h$. So let's say the mound has a radius r = 10 cm and its height = 19 cm. Given that π = about 3.14, the added surface area of one tussock would = $\pi r^2 h$ = 3.14 x 100 x 19 = 5966 cm^2 and the total for 4.5 tussocks per square meter would = 26,847 cm^2. That would be nearly 2.7 m^2. Note that tussock-top areas are not added because that area is already part of the flat area. So 4.9 average-size tussocks could almost triple the surface area.



Carex meyeriana

Paspalum quadrifarium

However, scientists like Steven Hall want to see results of actual tests, not just coincidences. So, he added artificial tussock-size mounds to a field site and watched for species to establish. He found twice as many species where there were mounds than on flat soil. Tussock mounds *caused* greater diversity. Of course, more tests in more types of conditions could strengthen that assertion. Science progresses when ideas are discredited and when they are supported. Taller tussocks with more microsites allow more kinds of species. So tussocks likely increase species richness both by adding surface area and providing varied microhabitats.



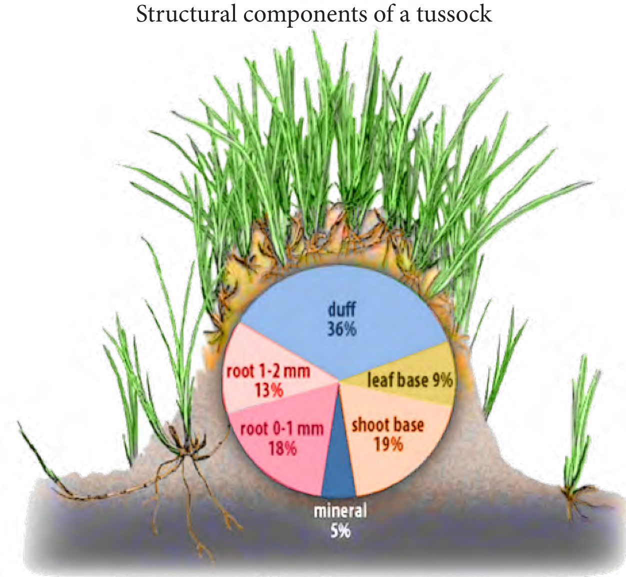
CRITICAL THINKING • What about *Carex sempervirens* in Swiss alpine grasslands, where more species occur around tussock bases than on tussock tops? Isn't that a conflicting pattern? No; not really. I think this finding actually supports ours, because the common influence is water stress—too much in our case, too little in Switzerland. I suggest that fewer upland species can tolerate the upland/dry alpine pasture conditions on tops of *C. sempervirens*, and fewer wetland species can tolerate the wetland/waterlogged conditions on bases of *C. stricta* tussocks in sedge meadows. In both cases, water level is a stress factor, so results do agree.

Second Ecosystem Service • Tussock sedge stores carbon. When carbon is "stored" it stays put; it doesn't move into the atmosphere, and it doesn't add to greenhouse warming. Thus, storing carbon is a major service that wetlands perform. Gradually, scientists are figuring out which wetlands and where the most carbon is being stored on Earth, and not released to the atmosphere. While a lot of carbon gets stored in sedge meadows as deep peat and thick, black organic soil, it also seemed that tussocks formed by *Carex stricta* would store a lot of carbon (C) in sedge meadows. Beth Lawrence asked, "how much?" for her doctoral research. Also, to prevent global

warming, the carbon can't just be stored temporarily, or even for a few decades; it must be stored long-term. So Beth's project grew to include the difficult work of determining how much carbon would likely to be stored in perpetuity.

In three unplowed *Carex stricta*-dominated tussock meadows in the Upper Midwest, Beth collected data on tussock size and composition to calculate how much C was present. This required field sampling and months of laboratory work sorting the materials that make up tussocks (see pie chart). Before she conducted her study, I had assumed that the tussocks were partly or mostly mineral soil, trapped in clusters of sedge leaves, rhizomes, and roots. Not so; they were mostly organic (95%)! Science progressed by rejecting an incorrect assumption.

Structural components of a tussock



In these meadows, the tussocks were tall (average = 17.2 cm) and large in volume (4,113 cm^3), so, yes, they accumulated organic matter (which contains C). The soil below and around tussocks also stored C, and in Beth Lawrence's study, the tussocks made up about half (41–62 %) of the total C in these sedge meadows. How long had the C been accumulating? To find out how old the tussocks were, Beth sent samples to a lab for bomb ^{14}C dating (based on ^{14}C content following ~1965 nuclear bomb testing). The tussocks were estimated to be >50 years old. Their long-term persistence is consistent with slow rates of leaf decomposition on tussocks (26% per year) compared to rates on moist soil between tussocks (39% per year).

Does restoration of *C stricta* match the amount of C stored in natural wetlands? Not in the short term. Beth Lawrence compared C storage in a restored meadow and an urban meadow to the above three "remnant" tussock meadows (parts of larger natural wetlands). Beth found less stored C in the urban meadow with shorter and fewer tussocks and in a restored meadow (≤15 years old). It will take decades for such sites to store as much C as natural wetlands do. Her results support the need to conserve historical Tussock sedge meadows for C storage and other ecosystem services.

Do wetter hydroperiods assist tussock formation? In search of an answer, Beth Lawrence measured elevation in a field site with 4.9 tussocks/m^2 with an average tussock volume of 1160 cm^3 and mean height of 15 cm. Elevation was a proxy for water depth and hydroperiod (wet-dry pattern) in southern Wisconsin. Taller tussocks occurred at lower, wetter elevations, suggesting that roots and rhizomes grew vertically, above the anaerobic, waterlogged conditions. But, like other students in our research lab, she wanted to conduct a controlled test of water levels, as well as nutrient additions. So she set up a 3-year mesocosm experiment in "mesocosms" (she used large cattle watering tanks) and varied hydroperiods and addition of N+P. We concluded that Tussock sedge accumulates more organic matter and C with a wetter hydroperiod.

Tussock sedge grows well in 150-gallon stock tanks where water levels are easily controlled.

In our outdoor mesocosms with Tussock sedge seedlings with organic soil, the most obvious tussocks were formed by sedge plugs that were continuously inundated, compared to treatments with varied water levels. Also, N+P addition (15 g N/m^2 + 0.37 g P/m^2) increased overall productivity. After three growing seasons, the tussocks with 18-cm-deep water and N+P additions had grown 12 times as large (volume 3274 cm^3) as the smallest tussocks (275 cm^3), which barely grew with the lowest water depth and no N+P.

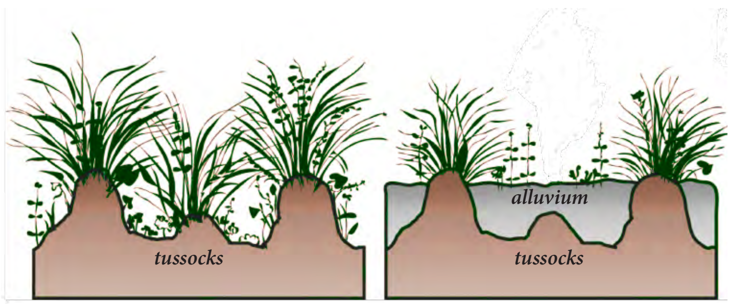
How "stored" is the C in Tussocks? In the lab, Beth Lawrence tested rates of decomposition for tussock biomass. She asked whether the organic matter actually *persists* (as stored C) or *decomposes* quickly. First, she cut tussocks into chunks of either leaf bases, fine roots, or duff. Next, she incubated each chunk and measured its release of carbon dioxide (CO_2) and methane (CH_4). The C left behind (not decomposed) was the **stable C.** For comparison, she measured C loss from five sedge meadow soils in the Upper Midwest (4 natural and one restored site). The C stored in tussocks and soil at the restoration site was the least stable. Restoration of stored C can take decades to centuries.

Once again, we learned that it pays to protect existing tussock meadows—the **C-storage service is not readily restorable.** Other authors agree that soil C is extremely slow to restore. If someone claims that degraded wetlands will restore quickly once the water is available, be sure to ask them, "What about the unacceptably slow restoration of soil C?"

Third Ecosystem Service • Tussock sedge reduces flooding. Imagine a storm with heavy rain. How would the rainwater flow, where would it flow, and how would it change as it makes its way downslope? Let's suppose it flows across a paved street—an urban feature that we call *hardscape* because it keeps water from soaking into the ground. Rain would flow fast and collect a lot of dirt and other materials, washing them into a gutter or ditch, which could lead to a precious wetland. Now imagine a tussock meadow in the same place. Rainwater would be soaked up by litter attached to tussocks. Water flow would be slowed by both tussocks and litter. The soil would absorb water and allow it to move belowground **(infiltrate)** as a trickle.

Wetlands are often compared to sponges. Flood protection benefits are worth millions per year. For example, in 2016, Vermont researcher Keri Watson and collaborators estimated the value of flood protection for one watershed affecting Middlebury (Otter Creek floodplains in Vermont) to be more than $126,000/year and maybe as high as $450,000/year. And in China, a 2017 government project offered several pilot cities $60–$90 million per year for 3 years to become **"sponge cities."** In other words, cities were paid to function like sponges—to create wetlands where soils and plant litter and roots could absorb water and later allow it to evaporate. The aim is to reduce floodwaters and, at the same time, cool urban surfaces. The Chinese government valued those services at up to $270 million for a single city! At the same time, the wetland would trap some of the particles and the water should be cleaner as a result…leading to the next service.

Fourth Ecosystem Service • Tussock sedge cleans stormwater runoff. As water flows across fields and streets and other surfaces, it collects mineral and organic materials, some of which infiltrate and some of which flow downstream toward wetlands. Where there are sedge meadows in the watershed, the water has opportunities to be cleaned—through **physical, chemical,** and **biological** processes.



Conceptual drawing of species loss following sedimentation

Consider a tussock meadow's **physical processes:** As dirty water slows down, sand, then silt, and then clay particles settle out of the water (collectively the **alluvium**). This is great for cleaning the water, but when too much mineral matter accumulates in a sedge meadow, it can smother the tussocks. Katy Werner found 0.4 to 1.3 meters of accumulated sediment in three Madison wetlands that collected sediment from their upstream watersheds, with greater deposition at the inflow of stormwater. She calculated a loss of one species per 1000 cm^2 of lost tussock surface area, and a loss of 1.2 species for every 10 cm addition of sediment over the buried organic-rich native (*histic*) soil. Alluvium also changed the quality of the surface soil by reducing the proportion of organic matter content and increasing the weight per volume (*bulk density*). A good design for a stormwater treatment wetland would include excavating a forebay to collect the larger particles (sand)—in an accessible location for frequent removal.

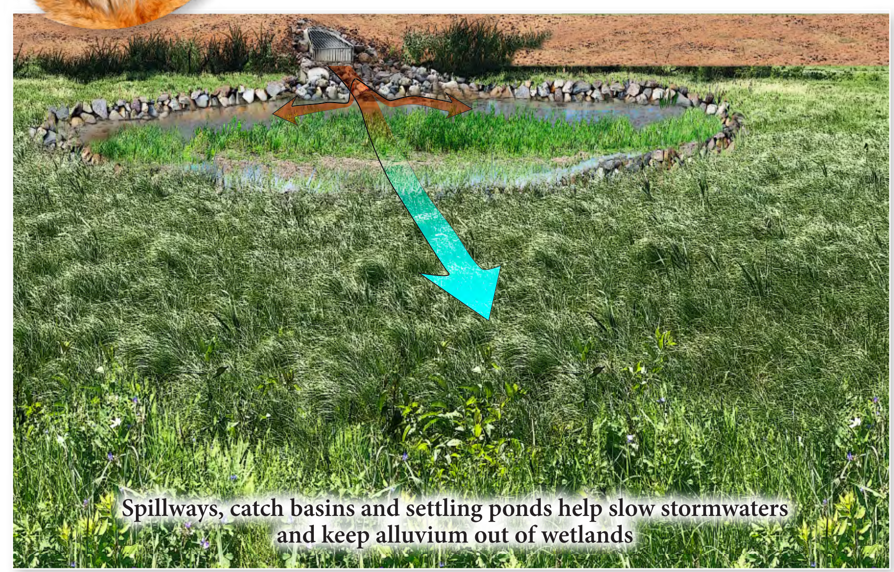
Further stormwater cleaning takes place via **chemical processes** (volatilization, adsorption, oxidation, reaction with light) and **biological processes** (uptake of nutrients; decomposition by microbes, and recycling of elements). In general, every material that we send downstream can be modified as it is carried toward a

wetland. Stormwater treatment wetlands are often required to remove toxic substances. This is possible where plants take up nutrients and specialized bacteria and other microbes decompose organic matter, remove nitrogen, and denature methane (see Fifth and Sixth Services below). Like the deposition of alluvium, the removal process is good for the surface water but the contaminants can be harmful to the stormwater treatment wetland that removes them. A trap or forebay could help collect grease, oil, and other persistent pollutants.

Why would tussocks improve water quality? A large part of being a superplant in a tussock meadow is having a *greater surface area compared to flat wetlands.* As calculated earlier, the meadow surface area can be 40% greater where there are 4.5 sizable tussocks per square meter, which suggests the potential for ~40% more absorbing and cleansing power—although that relationship needs to be tested. In general, Mr. Clean might "leave a sheen where you clean", but Tussock sedge has the edge; that's our pledge. It's a superplant, after all.

Who keeps track? For maximum water quality improvement in and around urban and agricultural lands, someone needs to be responsible for monitoring the accumulation of materials and for timely clean-up.

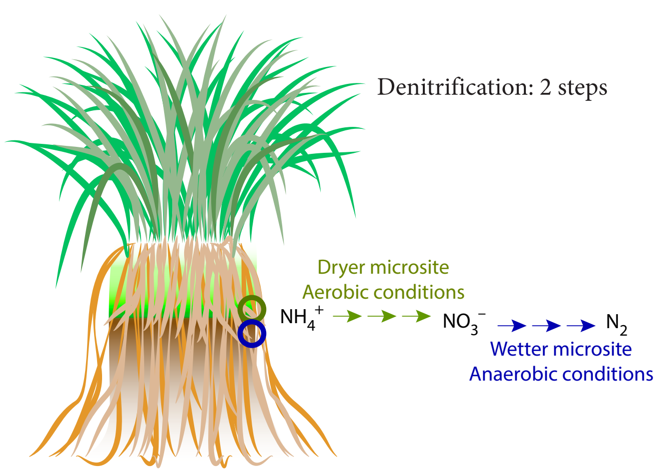
Neighborhood watchdogs are needed—people who know whom to call when there's a spill or overflow from a collection site.



Spillways, catch basins and settling ponds help slow stormwaters and keep alluvium out of wetlands

Fifth Ecosystem Service • Tussock sedge removes nitrogen: ***Denitrification.*** A common target for wetland restoration is the removal of excess nitrogen (N). That's because excess nitrogen causes invasive weeds to expand across wetlands and bluegreen algae (cyanobacteria) to "bloom" in lakes. Yuck! Agricultural landscapes are notorious for leaking nitrogen into downstream lakes, because N-containing fertilizers are added to crops every year. The same is true for many lawns. Before all the N can be taken up by the intended crop, a lot of the fertilizer can flow off the field and downstream to a wetland.

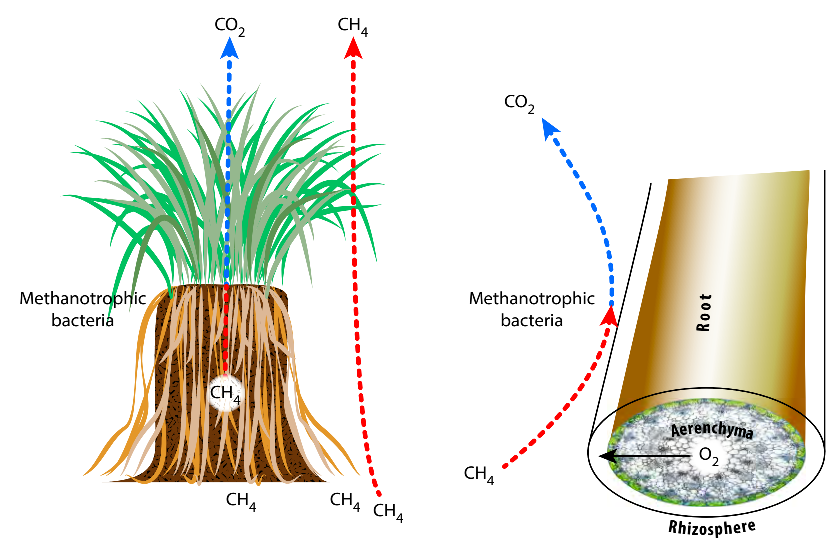
Denitrification is a unique and valuable process, because the nitrogen is removed from the ecosystem and released to the air! We understand N-removal well enough to create "treatment wetlands" to help remove both nitrogen and phosphorus (N and P) from runoff water. If we make such wetlands *large* relative to the watershed that leaks nutrients, and *bumpy* (topographically heterogeneous, with added soil surface area), they can remove more N! That's because the bumps have microsites that differ in hydrology, vegetation, and soil chemistry. As described at the beginning of this chapter, both aerobic and anaerobic conditions are needed for the **two steps in the denitrification process.** Simplifying, aerobic conditions promote **step 1** (convert ammonium to nitrate: NH_4^+ to NO_3^-) and anaerobic conditions promote **step 2** (convert nitrate to harmless nitrogen gas N_2). On bumps and tussocks, aerobic and anaerobic conditions occur in close proximity. Microtopography makes a difference!



Sixth Ecosystem Service • Tussock sedge oxidizes methane. Methane (CH_4) is a naturally occurring compound that is released from wetlands, particularly peatlands with high water levels and anaerobic substrates. Microbes that release CH_4 are called *methanogens.* Methane is consumed by other microbes called *methanotrophs* that can oxidize CH_4.

What's wrong with methane? It's a major cause of global warming, even though it is less common in the atmosphere than carbon dioxide (CO_2). That's because it has very strong heat-trapping ability (far more than that of CO_2). When methane reacts with oxygen (*oxidation*), the carbon is still released, but it is released as CO_2, which is less harmful than methane (about $^1/_{25}$ as much).

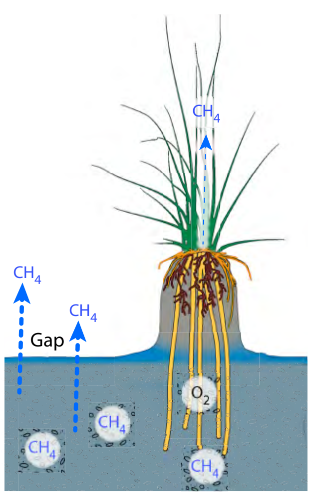
Methane oxidation is a major ecosystem service that occurs where roots with *aerenchyma* leak air (containing oxygen) into the roots' immediate vicinity, called the *rhizosphere,* as well as in tussocks where methane moves up to the tops and the air flow helps methanotrophic bacteria oxidize methane. Methanotrophs help reduce global warming by converting methane to carbon dioxide. Less methane emission is a good thing!

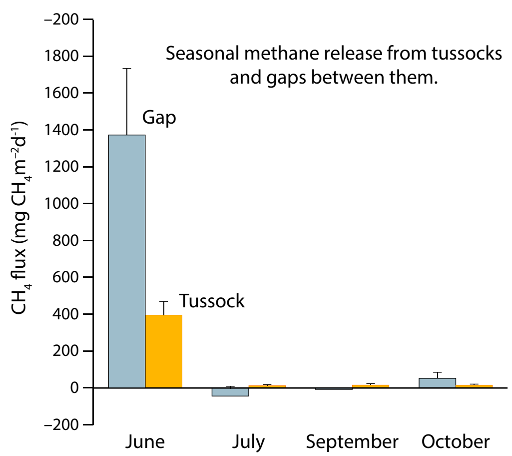


Methane is released from wetlands
and oxidized to carbon dioxide by biological processes.
Methane emissions vary greatly in relation to water levels.

When methane (CH_4) is produced by anaerobic bacteria (methanogens) in the soil, that gas can move upward to the air through plant tissues that have ample aerenchma. But that's not all; it's a two-way path, because oxygen in the air can also move downward through aerenchyma, allowing CH_4 oxidation. It is well known that some wetlands often release methane, while others rarely do. Wetland ecologists have debated the reasons based on their own readings and experiences with different hydroperiods and different vegetation.

So how do tussocks affect methane emissions? Researchers are just beginning to find out. Only recently have "controlled" comparisons been made in places with the same climate and weather, but with large differences in water levels. Where might that occur? That's right—wet meadows with sedge tussocks and interspaces without tussocks. Two studies explored methane emissions by comparing tussock tops and gaps between tussocks—one study in the Czech Republic and one in Wisconsin. Both research sites have temperate climates. The results agree that a great deal of the variation can be attributed to tussock structures, where the tops remain above the water, while gaps have wetter soil, ranging from flooded to unflooded.





Beth Lawrence compared tussock tops and inundated soil interspaces at Cherokee Marsh and documented differences in methane release. Tussock tops released less methane (393 ± 76 mg CH_4 m^{-2} d^{-1}) than inter-tussock substrates (1362 ± 371 mg CH_4 m^{-2} d^{-1}). Tussock tops are sites of methane oxidation, and tussock topography can reduce greenhouse gas loss by allowing methane to be oxidized as it moves up through a tussock.

Researcher Vítková Jitka and her collaborators compared methane emission from tussocks and gaps between them. Most CH_4 fluxes were greater from tussocks than from gaps, because aerenchyma "ventilates" the roots and soil. At other times, greater fluxes from a gap occurred when water levels were above the soil surface.

Seventh Ecosystem Service • Tussock sedge can fix nitrogen. It might seem odd to highlight N-fixation, when N-removal (#5) is also listed as a service. However, tussocks perform a service by removing excess N when a wetland is so N-rich that it favors weeds. In contrast, N-fixation is a service when N is in short supply. Cyanobacteria with special anaerobic cells with thick cell walls to exclude oxygen can fix N. Also, a few native wetland plants (notably legumes) support **N-fixing bacteria** among their roots, and the bacteria convert N_2 in air into usable amino acids in root cells. Wow! That's important, because all plants and animals need amino acids, and while there are tons of N_2 molecules in the Earth's air, only a few cyanobacteria and a few higher-plant species can turn N_2 gas into usable N as nitrates, ammonium, and amino acids. N-fixation is an ecosystem service where N limits the growth of desired plants.

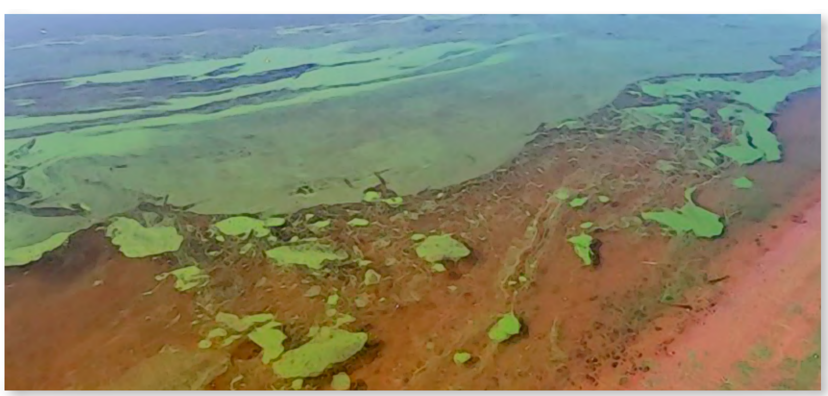
N-fixing nodules on roots of a soybean plant

How does Tussock sedge trap and "fix" N? According to a study by Eckardt and Biesboer in Minnesota, N-fixation occurred in soil cores with *C. stricta* roots along an undisturbed lakeshore. Later, a study by Wickstrom and Garono of Ohio peatlands found evidence of N-fixation in soil cores surrounding many vascular plants, including *C. stricta*. But such studies of soil and peat cores do not separate microbes that happen to co-exist with other organisms from those that might be fixing N in association with the roots of Tussock sedge. The N-fixation might be caused by microbes in the rhizosphere, the soil, or endophytes in root tissues.

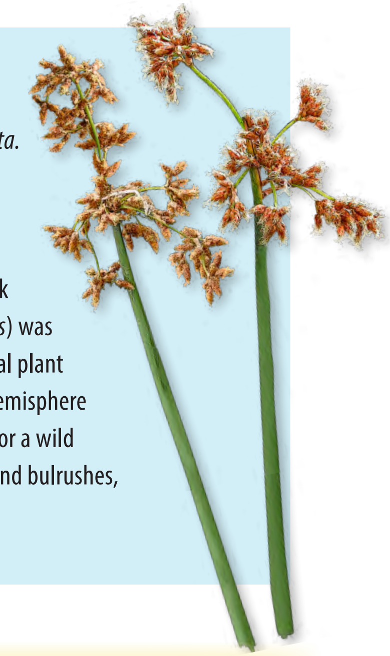
$N_2 \longrightarrow$ $NH_4^+ + NO_3^-$ $\longrightarrow$ Amino acids $\longrightarrow$ Proteins

N- fixing bacteria   Plant cells

Nitrogen in the form of nitrates is so important that people figured out how to "fix" N artificially, and it was used in explosives during World War I. Soon afterward, artificially fixed N-containing fertilizers experienced "explosive" growth. Now, excess human-fixed nitrates run off the corn fields and pollute downstream waters, causing algal blooms and a dead zone in the Gulf of Mexico. Yikes: Some bloom algae (specific strains of cyanobacteria) make the water toxic to people, pets, and some wildlife. As I write this in September 2021, Lake Superior is experiencing its first toxic cyanobacteria bloom in the Duluth-Superior harbor—not the first algal bloom in this lake, but the first toxic bloom. The toxic cyanobacteria are likely the kinds that lack anaerobic cells (heterocysts with the ability to fix N). When N becomes available from urban runoff or fertilizers applied to the land, the cells and colonies respond by reproducing exponentially, which we call a "bloom." Sad news, especially when the cyanobacteria are a toxic strain! Too much N-fixation by people, with widespread use on lawns and crop fields, is not a good thing.



Toxic cyanobacteria bloom in Duluth-Superior harbor.
Photo: Hannah Ramage • Lake Superior National Estuarine Research Reserve



Lathyrus palustris is a preferential native plant associate of *Carex stricta*. This legume might fix nitrogen in *C. stricta* tussocks! Who will be first to explore this possibility? Recently a close relative of Tussock sedge, California bulrush (*Schoenoplectus californicus*) was shown to fix N, resulting in ~14% to 32% of the total plant N among samples from 8 sites across the Western Hemisphere (Rejmánková et al. 2018). These are relatively high values for a wild plant, and they justify more research on N-fixing bacteria and bulrushes, not just sedges.

CRITICAL THINKING • How many foods do you eat from plants that fix nitrogen? Are beans, peas, and lentils part of your diet? How about twice-cooked beans (frijoles refritos)? Do you eat them because they are high in protein? How much protein did you eat from plant sources this week?

"Bean there, done that"!
Legumes, members of the bean family (Leguminose) are well known for performing the N-fixing service. Once fixed (incorporated into amino acids), the legumes can pass usable N on to other plant species, through decomposition and leakage to the soil. The legumes that we eat (such as beans, peas, and lentils) contribute amino acids to microbes, people, other herbivores and omnivores. It's no coincidence that legumes are high-protein seeds; with more amino acids, they can make more proteins.

"ordinary" corn aerial roots

corn aerial roots secreting gel

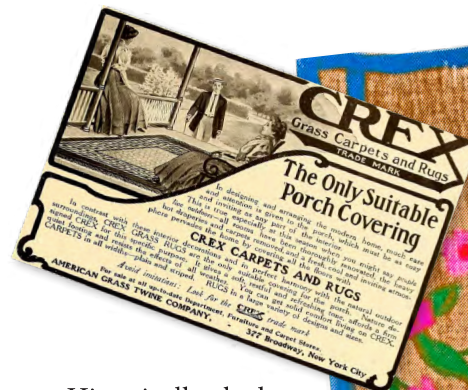
Varieties of corn from Oaxaca, Mexico, secrete mucus-like gel from aerial roots along the stalk. The gel excludes oxygen and provides sugar to bacteria, which fix atmospheric nitrogen into a form that fertilizes the plant.

Wouldn't it be great if all crop plants had their own N-fixing microbes so N could be fixed as needed? Corn croplands would produce less N-rich runoff if the plants were fixing their own N. However, corn is a grass and grasses don't usually have root nodules with N-fixing microbes. **Or do they?**

There's at least one strain of perennial corn in southern Mexico that grows finger-like projections along its stems. The fingers are coated in a sticky gel that supports—you guessed it—N-fixers! But; it's too soon to celebrate. A lot of research needs to be completed before such plants can be grown in Wisconsin's soils and climate.

Eighth Ecosystem Service • Some sedges produce useful fibers. Sedges are not known for providing edible plant parts, but there are other uses. In California, Dr. Michelle Stevens studied White root sedge (*Carex barbarae*), which grows long **rhizomes** that Native American have used in basketry for centuries. Along rivers, more than 20 tribes of California Indians removed other understory plant species and transplanted the White root to create productive monocultures. Plants were grown ~1 m apart with rhizomes up to ~2 m that were harvested at intervals of 3 years in a Traditional Resource Management system.

White root sedge basket
Photo courtesy Michelle Stevens



Historically, the long narrow leaves of Tussock sedge and other native sedges were harvested to weave rugs and chair seats, e.g., in Wisconsin and Minnesota, the Crex Carpet Company mowed sedge meadows and harvested sedge leaves from a 30,000-acre wetland (Crex Meadows) that is now a wildlife conservation State Wildlife Area (https://www.crexmeadows.org/).

A few wetland "distant cousins" of sedges provide foods: Wild rice (*Zizania aquatica*) is harvested in Minnesota and Wisconsin, along the shore of Lake Superior. Two other foods are Swamp potato (*Sagittaria latifolia*), which has edible tubers used by Native Americans, and Water chestnut (*Eleocharis dulces*), which has edible corms that we import from Asia. These food plants are cultivated using prolonged hydroperiods, more like aquatic species than a sedge meadow.

Ninth Ecosystem Service • Tussock meadows support wildlife, which benefits millions of people who watch birds, enjoy deer hunting, photograph or paint/sketch animals, or simply appreciate native animal life. Tussock meadows support uncounted animal species, contributing to overall biodiversity. Not nearly enough is known about the insects, amphibians, birds, reptiles and mammals that call sedge meadows home. Studies of human impacts on wildlife and restorability of habitats are presented under Chapter 6 about restoration. Meanwhile, you can consult the Wisconsin Dept. of Natural Resources description of Waubesa Wetlands (dnr.wi.gov/topic/Lands/naturalareas/index.asp?SNA=114), which says, "Bird life is diverse and includes sandhill crane, green heron, marsh and sedge wren, blue-winged teal, green-winged teal, and willow flycatcher." My eBook, *Waubesa Wetlands: New Look at an Old Gem,* is on line free at the Town of Dunn, and hard copies are available at Dunn Town Hall, along with a newer, shorter version, *Waubesa Wetlands: A Quick Look.*

10+ ? Do tussock meadows provide more than 9 ecosystem services? Yes, if we add all the **cultural benefits** that come from inspiration and well-being, through art, music, sight-seeing, photography, sketching, and physical health while hiking, bird-watching, and canoeing. Ecosystem service is a flexible term, especially when considering cultural services—did I just list one service or many? The 9 functions numbered above are the most widely studied ecosystem services. They led me to the opinion that **Tussock sedge is a superplant!**

What are the services of Earth's ecosystems worth? Many scientists and economists have tried to answer this question. Here's a good example. In 1997, Robert Costanza and co-authors put dollar values on 17 ecosystem services for all biomes on Earth and calculated a global total of $33 trillion per year. Wow. Later, they updated their estimate based on changes in values and changes in land use areas. The 2011 global total for all biomes was $125 trillion/yr—almost four times their earlier estimate…. Quadruple WOW$! Note that the standard economic indicator, called the gross domestic product (GDP) was approximately $46.3 trillion/yr in 1997 and $75.2 trillion/yr in 2011. Those numbers do not include ecosystem services in the valuations of the world's economic status. Do you think they should? I do! Natural ecosystems often contribute more to the economy than GDP.

What proportion of services came from wetlands? As reported above, the 2011 estimate for the total worth of all services of all biomes was $125 trillion/yr. Of that, the proportion from global wetlands was $26.4 trillion/yr. That's over one fifth the total for all biomes. Knowing that wetlands cover **less than a tenth of Earth's surface area,** that's impressive! Wetlands are worth far more than their small area might suggest.

Which wetland services led to that total? In their 1997 estimate, Costanza and co-authors reported the worth of each wetland ecosystem service in 1994 $US. Here are the data for 10 services (these services are defined in the paper published in 1997).

Wetland ecosystem service	Dollars / hectare / year
Disturbance regulation	4,549
Waste treatment	4,377
Water supply	3,800
Cultural services	881
Recreation	574
Habitat/refugia	304
Food production	256
Gas regulation (e.g., CO_2)	133
Raw materials	106
Water regulation	15
Total	14,785

In 2017, Costanza and co-authors reflected on their earlier estimates:

> "Given the huge uncertainties involved, we may never have a very precise estimate of the value of ecosystem services. Nevertheless, even the crude initial estimate we have been able to assemble is a useful starting point (we stress again that it is only a starting point). It demonstrates the need for much additional research and it also indicates the specific areas that are most in need of additional study. It also highlights the relative importance of ecosystem services and the potential impact on our welfare of continuing to squander them." …. Above all, there is a need to broaden **public discourse and participation in integrating ecosystem services and natural capital into mainstream economic policy."**

Well stated! Now, how should we proceed?

Recent research in central China made strides in valuing ecosystem services and recognizing their contributions to the national economy. Stanford Professor Gretchen Daily and her co-author Ouyang were pleased to share key findings in the box on page 51. They add up the ecosystem services to obtain the gross ecosystem product (GEP) and show that GEP can exceed the gross domestic product (GDP). This is a new way forward!

Tussock sedge can't take credit for all the ecosystem services in a tussock meadow. Dozens of other plant species will be working alongside it. Even species that don't form tussocks will benefit from the one that does! What are those other species and what determines their presence in tussock meadows?

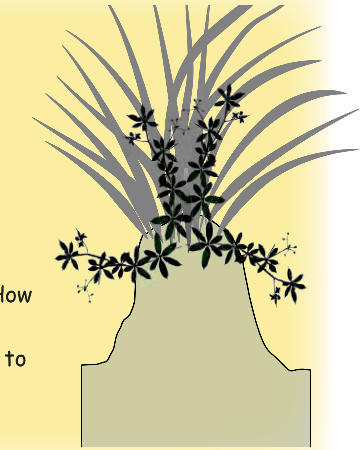
There are **two ideas** about the plant species that co-exist in tussock meadows—one that it just *depends on which species are nearby.* The other idea is that many species rely on some quality of tussocks. Early on, New Hampshire doctoral student Leonard Lord created several experimental tussocks and found that they were colonized by species that were present in a nearby wetland. Later, Lord and co-researcher Lee suggested that the seeds colonizing their experimental tussocks were produced by nearby wet meadow plants. Ecologists would say that **"propagule availability determined composition."**

The alternative idea is that co-existing s*pecies rely on some characteristic of Tussock sedge.* That conclusion came from Great Lakes wetlands, where several plant species were *"associated"* with Tussock sedge, with some appearing to *depend* on an overstory of sedge leaves. In these wetlands, tussocks averaged 19 cm tall and sedge canopies "hogged the light." Did that benefit other species, or did they just tolerate shade? More analysis was warranted. The highly qualified wetland ecologist, Carol Johnston, rose to the challenge.

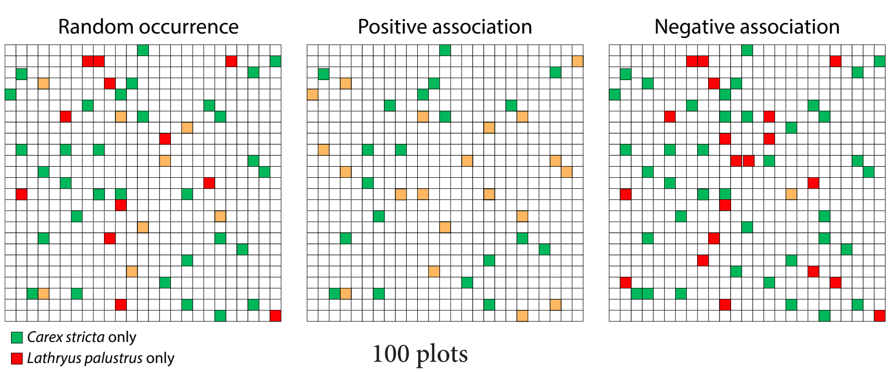
Using an electivity index, Johnston identified 12 plants that "preferentially occurred" with *C. stricta,* as follows:

- Four had draping stems (Marsh bellflower, *Campanula aparinoides;* Bedstraw, *Galium trifidum;* Tearthumb, *Polygonum sagittatum;* and Marsh pea, *Lathyrus palustris*).
- Five were shade-tolerant forbs (Sweet flag, *Acorus calamus;* Water hemlock, *Cicuta bulbifera;* Touch-me-not, *Impatiens capensis;* Tufted loosestrife, *Lysimachia thyrsiflora;* and Marsh skullcap, *Scutellaria galericulata*).
- Two were grasses (Fowl bluegrass, *Poa palustris;* and Bluejoint, *Calamagrostis canadensis*).
- One was another sedge (Lake sedge, *Carex lacustris*).

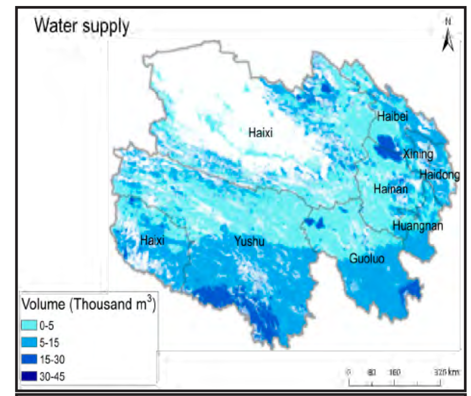
CRITICAL THINKING • Why might some species co-occur preferentially? Do they use the same resources in different places? If a draping species relies on an upright sedge for physical support to grow upward into the light, the sedge would be facilitating the "draper." How might shade affect a frequently co-occurring species? How does shade tolerance differ from a shade-requirement? Can you think of experiments to test for tolerance vs. requirement?



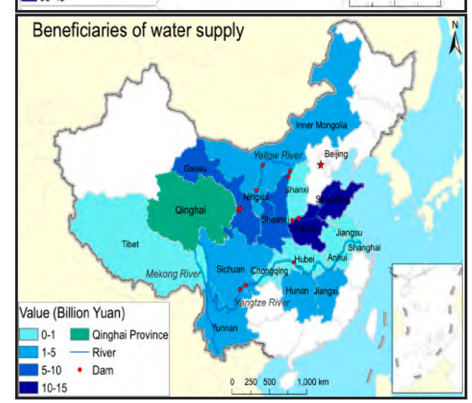
How do we test for associated species? Ecologists often ask whether co-occurrence of two species is random or associated (Note that species can be positively associated by co-occurring together more often than at random, or negatively associated by "avoiding each other"). A simple approach is to organize data for pairs of species into 2 x 2 contingency tables and apply Chi-square tests. Here's the logic: If we sample 100 plots, and we find *C. stricta* (Cs) in 40 and *Lathryus palustris* (Lp) in 20, how many plots would have both species if both are distributed at random? In this hypothetical example, Cs occurs in 40% of the randomly sampled plots, so 40% of any set of plots should have both species, i.e., 40% of the 20 plots with Lp = 8 plots. Eight co-occurrences would be random. If, instead, Cs and Lp co-occur much more often, say in all 20 Lp plots, they would be **positively associated**, and if they only co-occur in 1 or 2 plots, they would be **negatively associated.** Further research would be needed to learn why such patterns were found.



A new way forward • Decision-makers should use the *Gross Ecosystem Product* **(GEP)** in addition to the *Gross Domestic Product* (**GDP**) to evaluate the status of the economy. **GEP measures all the ways that nature supports economic activity and human well-being.** In Qinghai Province, China, where three great rivers (Mekong, Yangtze, and Yellow) originate, there are many water-related services at high levels. There, GEP actually exceeded GDP in 2000.



Qinghai Province



China
Qinghai Province shown in green

Maps courtesy of Z. Ouyang, G. Daily and co-authors (see Ouyang et al. 2020).

Case study • A multi-disciplinary research team estimated the monetary value of ecosystem services of Qinghai Province and mapped their sources. This province is called the "the water tower of Asia" because it supplies 47.0 billion cubic meters of water annually, benefiting agriculture, hydropower, industry and domestic users throughout much of China. Not surprisingly, water supply was Qinghai Province's most important ecosystem service in 2015, contributing 57.6% of its GEP. The 2020 paper by Zhiyun Ouyang and a dozen co-authors features these two maps (and 16 more) of the province and its services/beneficiaries. Stanford University Professor Gretchen Daily is the senior author of the paper. She was among the first ecologists to promote ecosystem valuation (see history in a 2017 paper by Costanza and co-authors).

Summary • This chapter emphasizes nine ecosystem services that Tussock sedge and tussock meadows add to wetlands.

The number of services is less important than how valuable each one is. To my knowledge, no one has estimated the dollar value of tussocks, but I did estimate that 4.5 tussocks in a square meter could more than **double the surface area** of a flat meadow. So if services increase with area, twice as much surface area **could double the functioning** of a wet meadow. Some tests of such predictions are needed! I also don't know of anyone who has tested species that co-occur on a tussock to see if they facilitate growth and reproduction of one another. Consider the September canopy from our *Temporal segregation* illustration. Does the purple Aster stabilize the *Carex stricta* leaves so they remain upright and photosynthetic rather than get packed down as litter? Does *Mentha arvensis* emit enough minty odor that it wards off insects that might otherwise attack other plants? There is much to learn.

September

Now that you are well acquainted with Tussock sedge and its meadows, I hope you share my opinion that this once-widespread native sedge is a **superplant** for providing essential ecosystem services. As humans, we probably won't admit that we can't live without it, but perhaps we can all can agree that people spend a lot of money trying to live *without* wetlands. Engineers excavate drainage channels and build levees to compensate for lost flood abatement services; cities build treatment facilities to clean the surface water; public health watchers close our swimming beaches when our lakes develop cyanobacteria blooms; we all anticipate the damages that continued global warming will spawn, which we all need to try to prevent from happening. In the next chapter, let's consider when and why we lost so many tussock meadows and how we can move forward and simultaneously learn to restore them. In Chapter 6 we proceed to replant and rehabilitate former tussock meadows (I call it *adaptive restoration*).

5
When and why were so many wetlands lost?

Sedge-dominated wetlands were much more extensive historically than now. Long-term losses of wetland acreage across the Nation's 48 contiguous states were estimated by the US Fish and Wildlife service. Senior scientist Tom Dahl's calculations were based on changes between maps from the 1780s and areas identified as wetlands on aerial photos in the 1980s. Over those 200 years, the nation's contiguous 48 states lost 53% of their wetland area. **Where?** More than 20 million acres of wetlands were drained in Ohio, Indiana, Illinois, and Iowa alone. Each of those states lost 80% or more of its wetland area. **Why?** Most of the losses in the Upper Midwest were attributed to drainage for agriculture. Indeed, a major industry was devoted to draining wetlands, involving factories to make millions of drain tiles, machines to excavate ditches, specialized digging equipment to bury the tiles, and workers to install them.

Demonstrating tile installation in Saskatchewan

One contemporary restoration practitioner, Tom Biebighauser, wrote an entire book about Wetland drainage, restoration, and repair.

In Wisconsin, the wetland area lost was only 46%, but "only 46% loss" is still a lot, especially when wetland losses continued along with declining quality of the wetlands that remained.

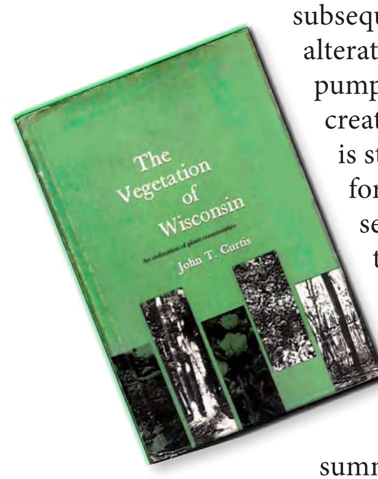
What was lost in southern Wisconsin? Fourteen Wisconsin counties that had many wetlands were inventoried using 1950s aerial photos. Researchers with the Game Management Division counted 25,000 wetlands totaling ~570,000 acres. Of the seven types of wetlands that could be identified and mapped from aerial photos, 55% of the total wetland area was called "fresh meadows"—which included sedge meadows. The researchers found and mapped 10,492 fresh meadows on the 1950s photos. What a task—before computers could do much of that work! Because they had data from an earlier survey using 1930s aerial photos, they could calculate wetland losses over three decades. Losses ranged from ~11.7% to 62.5% per county, with an overall loss of 24.7% (= 746,049 acres in the 1930s minus 562,001 acres in the 1960s). Top losers (in area—and we can also assume lost functions) were the counties of Kenosha (62.5%), Green (54.8%), Rock (39,9%), and Dane (33.7%). The winners were Jefferson and Columbia Co., with just 11.7 and 13.1% loss, respectively.

CRITICAL THINKING • The Game Management researchers also tallied the numbers of wetlands by size in the 1950s and again in a new survey based on the 1978 aerial photos. Can you predict the pattern? You'd be on the right track if you said that large wetlands were losing out by being made smaller, probably by drainage around the edges or by being dissected by roads. Meanwhile, remnants of wetlands increased the numbers of small (< 10 acres) wetlands. The number of wetlands under 10 acres doubled. Of course, we don't know the causes, but the pattern is suggestive. With help from Dr. Ken Potter, I summarized changes in numbers of wetlands in each of 5 size classes:.

year	Size, acres: 1 to 10	11 to 20	21 to 40	41 to 80	>80
1950s	13,888	3,652	2,655	1,535	1,201
1978	27,666	6,782	4,440	2,078	1,214

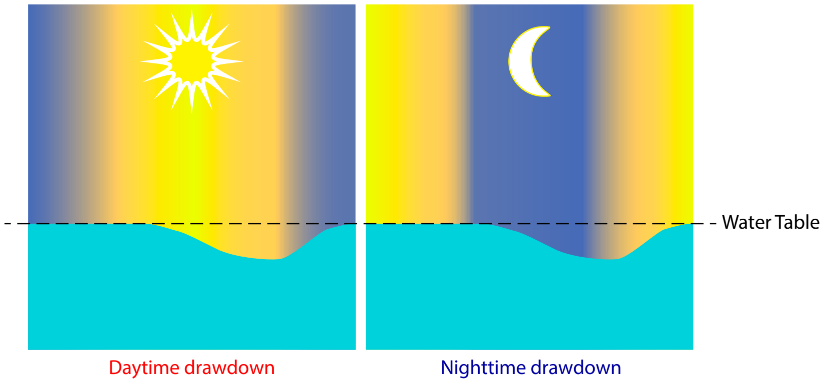
Number of wetlands

The Arboretum lost fens and sedge meadows. The UW–Madison Arboretum was set aside in 1934 to be a showplace for restoration research and practice. Regrettably, the Arboretum's two fens, both featured in the *Vegetation of Wisconsin*, were subsequently degraded due to hydrological alterations. For example, high-capacity wells pump groundwater for the City of Madison and create a "cone of depression" belowground that is still expanding due to increasing demands for water by a growing city. With reduced seepage of low-nutrient groundwater into the fens, their altered hydrology allowed aggressive plant invasions.



In 1998, when I arrived as UW's Aldo Leopold Chair of Restoration Ecology, it was already clear that **Wingra Fen** near Wingra Woods was losing its summer supply of groundwater. The probable cause was night-time pumping of groundwater to irrigate the adjacent Nakoma Golf Course. The golf course was implicated because our water-level meter recorded a night-time drop in the near-surface water and recovery the next day. Normally, groundwater levels drop in the daytime, when plants transpire the most, and water levels recharge at night. By 1998, Wingra Fen had lost most of its native plants as the local invasion of Reed canary grass expanded and outgrew them.

Night sprinkler



South Shore Fen was in worse condition than Wingra Fen. Located on the south edge of Lake Wingra, a small, eutrophic lake, this fen used to be visible from a canoe. Then it became dominated by invasive Buckthorn (*Rhamnus cathartica*). Today, the former fen is difficult to re-locate.


Buckthorn

South Shore Fen and Dr. Quentin Carpenter pointing out where Cattails and Reed canary grass invaded after Buckthorn was blown down.

The loss of both Wingra Fen and South Shore Fen adds more evidence to the widespread pattern that wetland types are controlled by *hydrology*, i.e., both the timing and quality of water supplies. Here's another example from the Arboretum, this one about a sedge meadow that converted to invasive Cattails.

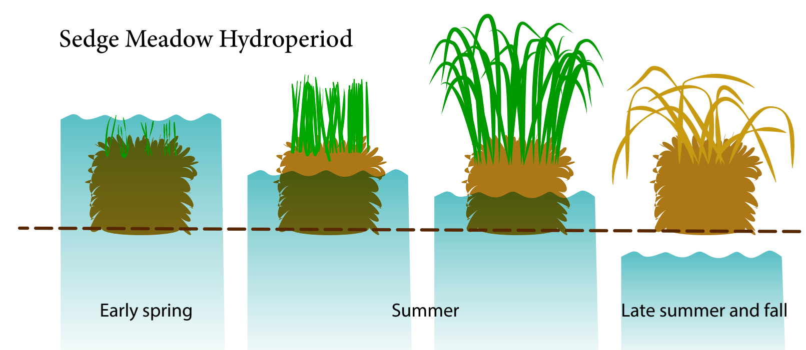
Gardner Marsh, east of Lake Wingra, was once a large, diverse sedge meadow. For her M.S. thesis, Harriet Irwin surveyed the site in 1970 and 1972, when it supported 108 plant species, including several sedges (*Carex* species); Bluejoint grass, *Calamagrostis canadensis*;


Natives

Hybrid cattail • Note gap

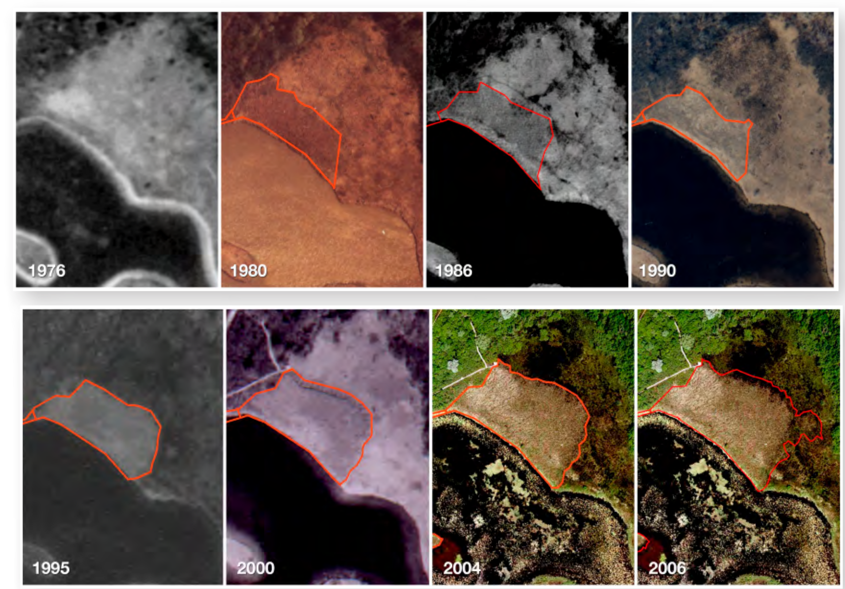
and the native Cattail, *Typha latifolia*. Several rare plants that were reported in the 1930s had already disappeared, according to Irwin. Since then, the hybrid *Typha* x *glauca* replaced >12 ha of diverse sedge meadow vegetation. While we don't know how fast Cattails expanded across Gardner Marsh, we do know that *Typha* clone diameters can expand 4 m per year (2 m radius expansion) when growing behind a dam (which stabilized water levels, studied by doctoral student Aaron Boers). Further evidence of Gardner Marsh's shift from a diverse sedge meadow to an invasive Cattail marsh was found by graduate student Steven Hall, who interpreted historical aerial photos that showed where and how fast the hybrid Cattail was replacing sedge meadow vegetation.

Steven Hall learned that in 2007, the Cattail marsh had >75% cover of hybrid *Typha*, while the remnant sedge meadow had an average of 4.9 species/m^2. Species with more than 50% cover in 1–m^2 plots were: Water sedge (*Carex aquatilis*), Wiregrass (*C. lasiocarpa*), Lake sedge (*C. lacustris*), broad-leaved Woolly sedge (*C. pellita*), Beaked sedge (*C. utriculata*), the Bulrush (*Schoenoplectus acutus*), and Bluejoint grass (*Calamagrostis canadensis*). *C. stricta* was present, but not dominant. The canopy was formed by 2–3 species. Under the canopy, the Bald spike rush (*Eleocharis erythropoda*) was nearly always present. The only common forb was the Tufted loosestrife, (*Lysimachia thyrsiflora*). If you're wondering if any of these common sedges besides *C. stricta* produce tussocks, the answer is no; their rhizomes spread laterally to form continuous canopies. All are common in wetter conditions, with longer hydroperiods than the sedge meadow drawdown.



Tufted loosestrife and sedge meadow sedges (other than Tussock sedge) and their relatives.

The northern part of Gardner Marsh on November 21, 2005. Most of the herbaceous vegetation is invasive *Typha*. Box shows area studied below. ***Photo by Mike Healy***



Gardner Marsh, 1976–2008 showing expansion in *Typha* x *glauca* boundaries. Maps by Steven Hall

While stable water levels facilitate *Typha* growth, graduate student Isa Woo's field experiment in Gardner Marsh showed that adding nutrients alone could cause this conversion. I should point out that stable water levels can liberate nutrients in waterlogged sediments, so hydrology and nutrients do not act alone in causing and accelerating an invasion. Once established, the tall, "nutrient-gulping" invader easily outcompetes the native sedge meadow vegetation. Historically, we can assume that variable water levels favored sedge meadow and *Carex* dominance.

Tussock meadows were lost when Madison-area wetlands were drained and groundwater was usurped (slurped up) by high-capacity municipal wells. Such was the case for **Monona Wetlands Conservancy,** just north of Waubesa Wetlands. There, two municipal wells were drilled within 0.5 mile of the wetland in the 1960's. Computer modeling showed a 2 m drawdown in the sandstone aquifer and a 3–6 m drawdown in the surface water table. A large cone of depression (lowered water table caused by groundwater pumping) dried up springs, and depleted artesian aquifers. The winners were invasive Reed canary grass and aggressive Cattails; the losers were native plant species.

When did southern Wisconsin lose so much wetland area?

Wetland drainage in one southern Wisconsin county (Dane) was summarized in detail back in 1941 by Anton Frolik, who acknowledged the help of Aldo Leopold and others at UW–Madison, but who gave his address as Agronomy Department, University of Nebraska. Of Dane County's peatlands in the glaciated eastern half of the county, he tallied the loss of 45,020 acres that were deliberately drained in 18 large projects between 1900 and 1926. These "large projects" ranged from 680 to 5,000 acres, with an average project size of ~2,500 acres, and an average of ~1,732 acres per year. His paper in the prominent journal *Ecological Monographs* describes artificial drainage as "still in an immature stage of development," consistent with the view that wetlands were wastelands and needed to be drained—the sooner the better. However, Frolik condemned the deliberate use of fire to drive wildlife out of the wetlands. Apparently it was common practice "to remove unsightly vegetation and with slight success to control the composition of the vegetation." Frolik was aware that peat fires could easily burn deep into the soil, leaving only minerals and sand, hardly suitable for crops.

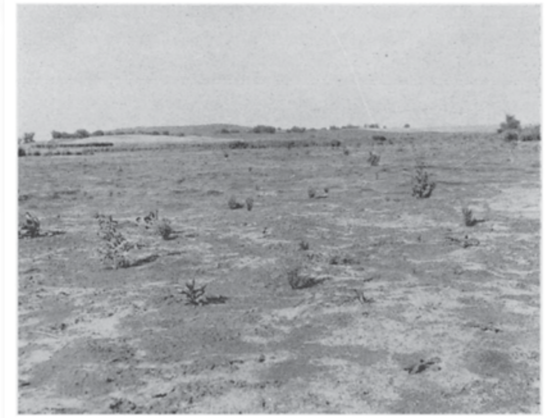


Fig. 22. A peat bed burned to a depth of several inches during 1934. Note the scarcity of vegetation. July 20, 1935.

Figure from Frolik's 1941 paper.

While Frolik's1941 study emphasizes Dane county's vegetation—both natural and altered by human disturbances—there is only one mention of tussocks and no separation of the county's many sedges into their various species of *Carex*. Sedges and rushes were described as associated, as were sedges and *Calamagrostis canadensis* (Blue joint, a native grass that provided pasturage and hay). However, tussocks and species associated with *Carex stricta* were the focus of an older, detailed, long-term study of several sedge meadows near Milwaukee, WI. Although Frolik mentions a 1936 study by ecologist David Costello, he devotes only a few lines to it, supporting his conclusion that tussock meadows are often monotypic *C. stricta*.

Fig. 4.—*Carex stricta* tussocks invading a pond

Figure from Costello's 1936 paper.

Costello's work deserves attention for its wealth of detail on Tussock sedge adaptations to varied water levels, tussock structure, sedge meadow species composition, and names of other natives in the Cyperaceae family and a dozen in the *Carex* genus. It seems that Costello (more than Frolik) could distinguish sedges in the field—not an easy task. A lasting impression of Costello's descriptive work is that tussock meadows were a common feature in the southeastern Wisconsin landscape and that several tussock meadows were very extensive, not just tiny remnants that escaped drainage.

In contrast with today's wetland advocacy, these early authors presented drainage and conversion as obvious management goals. Drained wetlands were viewed as more valuable for agriculture, grazing, mowing, and tree cutting (e.g., Tamarack, *Larix laricina*). With large drainage projects in Dane County and negative views of wetlands in general, it is notable that Wisconsin managed to retain over half of its pre-settlement wetland area.

spring, young cones

Tamarack swamps were drained and cut for their straight stems (boles), especially where other conifers were not available for settlers to build log cabins and other structures. Tamarack trees are notable for being deciduous, rather than evergreen, turning yellow and dropping their needles in fall.

fall, mature cones

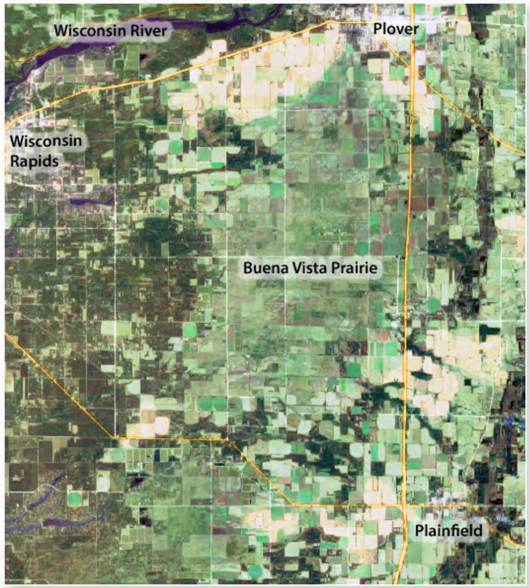
6
How can we restore tussock meadows?

Early restoration practitioners aimed to replace what had been lost. One of the first to use the term was George Perkins Marsh, who referred to the "restoration of disturbed harmonies" in 1864 and who advocated rehabilitation of damaged landscapes. Around the same time, land surveyors were busy describing the intact vegetation to mark section corners across the North American frontier. Wow! Surveyors criss-crossed Wisconsin in the mid 1800s and gathered quantitative data on the vegetation (especially trees) so they and others could relocate the corners of square-mile sections of land. The vegetation data were a fabulous spin-off that was later referred to as a description of the "original condition." And the existence of such a reference point made it tempting to adopt those data as goals for restoration in the 1900s.

CRITICAL THINKING • Is it realistic to plan to turn back the clock? Think of several reasons why the mid 1800s would and would not be suitable restoration targets for drained wetlands. Here's an example from my Masters' thesis research at UW–Madison: I located surveyors' hand-written notebooks for central Wisconsin at the State Capitol. I hand-copied the 1850s data on trees and other vegetation at every 1 x 1-mile section corner within the 10 x 10-mile Buena Vista Marsh. {Since then, the surveyors' data have been digitized and put online—Lucky you!}. By analyzing the data, I was able to map the historical vegetation as "marsh," Tamarack swamp, open Tamarack, and Alder swamp.

There are several reasons why Buena Vista Marsh would not be fully restorable, beginning with its altered hydrology. In 1850, that wetland had peaty soils. But subsequent drainage and cultivation dried the peat, which in turn fueled wildfires and left behind sandy substrates that challenged agriculture. What remains of the "good view marsh" is its name. Former wetlands, now uplands, are instead used for pastures and Prairie chicken management.

Restoration of peat would likely take centuries and might release climate-changing methane in the process. At the same time,



Buena Vista Marsh today. Left, North and South Buena Vista Wildlife Area. Below, Buena Vista Prairie Chicken Meadow.

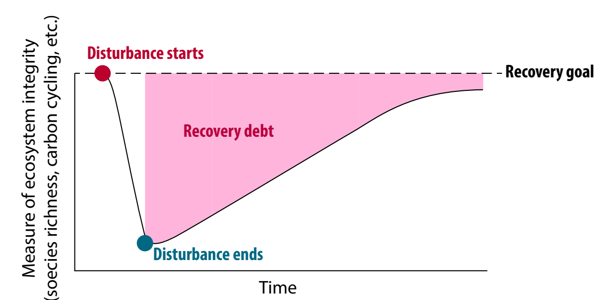
Map redrafted from Google Maps. Prairie Chicken view from Wisconsin Department of Natural Resources.

a warming climate would slow peat formation, by assisting the **decomposition** of organic matter instead of the intended storage. Historical hydrological conditions would also be difficult to restore, because such a large area was drained and there would not be much peat to soak up and retain water. So, to capture rainfall and groundwater, it would be necessary to block the drainage ditches for the water table to rise. But a rising water table would **drown** farm homes and agricultural fields in all areas that share the groundwater resource. And even if the peat and water levels could be recovered, the former vegetation would not restore itself, because there are no swamps left. So, tree nurseries would be needed, and experiments

would have to determine whether Tamarack would still grow in the sandy soils, while testing methods to re-convert agricultural lands to native vegetation. It's not impossible, but a regional approach would be needed to "replace what was lost."

Most highly degraded sites—and the altered watersheds that control their hydrology—have been modified in ways that are not easily reversed. In such cases, it is wise to begin with experiments to test our ability to provide suitable hydrology to recover wetland soil and vegetation. A few alternative targets should also be tested. Perhaps other native wetland species can grow in warmer, altered soils.

Are there ways to regain some of the wetland areas that have been altered across the Midwest? **Yes,** and wetland restoration is underway in many places by many proponents—even though there are likely to be "recovery debts." A focus on restoring appropriate hydroperiods for a sedge meadow (i.e., with a summer drawdown) could include tussock topography. Plans to plant native species could include a **superplant** and complementary species that can use different resources or the same resources at different times (spatial or temporal segregation).



Recovery debt • the shortfall between lost and restored condition. Dashed line = the goal (ecosystem recovers to a state existing either before disturbance or to that of a similar "undisturbed" ecosystem.

Experienced restorationists advise setting broad targets. For example, Texas A&M Emeritus Dr. Steven Whisenant focused his 1999 book on processes and landscape-scale approaches to restoration, and the 2005 Millenium Ecosystem Assessment gave the world a strong message to restore ecosystem services and biodiversity to sustain human well-being. These are general goals. To become more specific, Wisconsinites are fortunate to have an online "tool" for selecting potentially restorable wetlands in every watershed across the state and to predict their future ecosystem services. The tool is

Wetlands by Design, compiled by Nick Miller and his colleagues at The Nature Conservancy and the WI Department of Natural Resources, Now, by clicking a few computer keys, restorationists can find out which ecosystem services each potential restoration sites could likely provide. Wow! No other state has such a practical and important restoration planning tool (but the authors are working toward regional and national coverage). Does this sound too good to be true? If so, check it out at: https://dnr.wi.gov/topic/Wetlands/documents/reports/3_Wetlands_by_Design.pdf. Some former wetlands are potentially restorable; some are not (like those under buildings or streets). If we share the vision of restoration, we can engage stakeholders who are willing to consider restoration as advocates, volunteers, and active players. Today's restorationists are realistic. We know that few potentially restorable wetlands will be fully recoverable, due to limitations of the watershed and onsite constraints. We know there is usually a **recovery debt.** That means that the outcome of restoration will likely fall sort of the target. Harvard professor David Moreno-Mateos and co-authors concluded in 2017 that: "Compared with reference levels, recovering ecosystems run annual deficits of 46–51% for organism abundance, 27–33% for species diversity, 32–42% for carbon cycling and 31–41% for nitrogen cycling." We also know that some recovery is better than none, whether referring to lost species or functions.

Will restoration efforts be cost effective? Or maybe even profitable? I recently read a claim that "each US dollar invested in ecosystem restoration generates $30 in economic benefits". I wanted to see how that number was calculated, but the author, Bernardo Strassburg, did not cite a source in his editorial in *Science.* So, I did some sleuthing on the internet:

CRITICAL THINKING • I found a report by the World Resources Institute (Dickson et al. 2021), which also said "Every dollar invested in restoration creates up to 30 dollars in economic benefits"—and these authors included a citation: Ding et al. 2018. So I located the paper by Ding et al. and learned that it focused on forests and it gave a range of profits: Ding et al. stated: "Studies estimate that *every $1 invested in restoring degraded forests can yield between $7 and $30 in economic benefits*"—and they included this citation: Verdone and Seidl 2017. Next, I noticed that Verdone is an author on the paper by Ding et al., so it is likely that both papers used the same data. So the consistent claims for forests and for a $7-$30 range of benefits per cost are being quoted as though they *refer to all ecosystems* and that restoration projects always generate the *highest profit* of the range for forests. Let's call this "good-news inflation".

Was there harm in inflating the outcomes of restoration? Few people will fact-check the journal *Science,* so it's hard to say. I would like to believe the rosier outcome, but my science-based skepticism leads me to wait for more data. Here, my claim is simply that recent studies are calling attention to the economics of restoring ecosystem services and indicating that **benefits can outweigh costs of restoration,** at least for forests. Further fact-checking is warranted, and research is needed on measured benefits from ecosystem services of tussock meadows. With so few studies of tussock meadows and so few studies of their functions, it is premature to proclaim specific dollar values.

Invasion by aggressive non-native plants is a major challenge for wetland restoration. Invasive species are both a restoration target (we try to eradicate them) and a consequence of restoration activities (they like the way we disturb the canopy and soil). Where Reed canary grass (*Phalaris arundinacea*) or hybrid Cattail (*Typha* x *glauca*) have taken over former wetlands, their removal is often a restoration goal, along with reintroducing native plants and animals. At the same time, their re-invasion is often the unwelcome outcome, as found by Julia Wilcox and Steven Hall, students who planted native vegetation, only to watch the weeds retake their Arboretum restoration sites. Although restorationists often try to control invaders and reintroduce native species, planted vegetation often reverts to invasives. Invader removal is advised where the problem can be addressed on site. But if invasion was caused by nutrient-rich runoff from upstream sources, then a watershed-scale approach will be needed. And after invaders are removed, constant surveillance and weed pulling will be needed.

It helps a lot to test the **seed bank** (seeds stored in the soil) to find out if native species are present and might **self-restore.** That's done by collecting soil samples and allowing seeds to germinate. There was a surprise waiting for Christin Frieswyk when the seed banks of five Cattail-invaded wetlands turned out to be dominated by Purple loosestrife (*Lythrum salicaria*), another aggressive invader. This seemed "unfair", because Purple loosestrife was not common in any of the five marshes. However, others had shown that a single *Lythrum* could produce up to 2.5 million seeds!

Is weed invasion a threat to tussock meadows? We can hypothesize that species-rich tussocks will resist invasion better than species-poor tussocks, and there was such a pattern in *Carex nudata* tussocks in a small California stream. Species-poor tussocks had been invaded by three weeds (*Cirsium arvense, Plantago major,* and *Agrostis stolonifera).* But when Jonathan Levine tested for a cause-effect relationship, he found the opposite. He planted 65 tussocks with up to 11 native species, and then added seeds of the common invaders to each tussock. To his surprise, he found

more invaders establishing where diversity was greater! He suggested that weed invasion was controlled at the germination and seedling stages, where shading by plant cover reduced establishment, but that claim also needs testing.

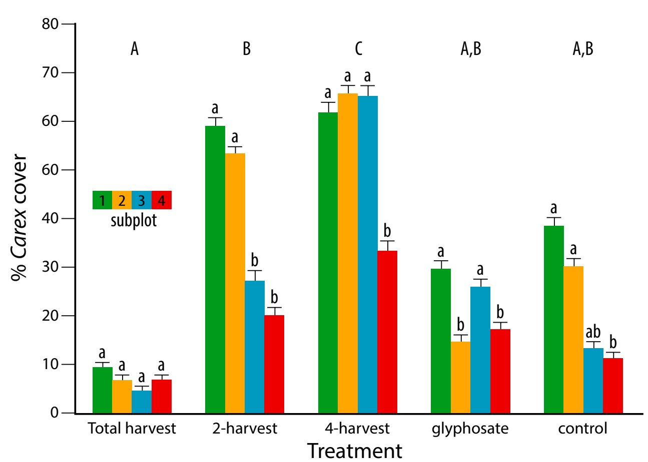
Tussock sedge is often overgrown by either Reed canary grass or hybrid Cattails, especially in nutrient-rich conditions. Tussock sedge is a poor match for invasive species that thrive with disturbance, especially where nutrients are abundant. Regrettably, despite its many "superplant" attributes, weeds tend to invade sedge meadows where agriculture and urbanization increase the flow of water, nutrients, and sediments. A combination of altered conditions and the arrival of highly aggressive alien species makes invasion more likely.

In seven Wisconsin *Carex stricta* meadows, Isabel Rojas-Viada documented the loss of half the resident species where Reed canary grass invaded. Her findings were verified at four "spatial scales" (using four plot sizes: 0.25, 1, 4, and 16 m^2). That guarded against a false outcome that an effect was detected only by a specific size of plot. In Rojas's study, the loss of species was consistent at all sampling scales.

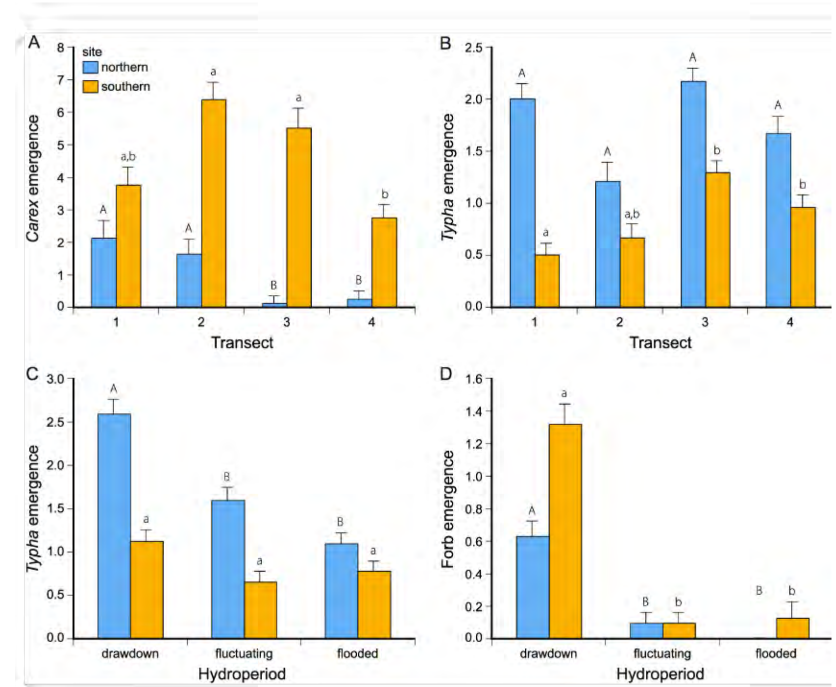
This outcome is similar to that documented for Cattail invasion in Gardner Marsh described earlier. In both cases, the invader is a taller plant than can capture light before it can reach Tussock sedge. Also, both invaders can capture nitrogen and use it to grow taller than Tussock sedge.

Can sedge meadows self-restore? Self-restoration is the recovery of the target vegetation just by reducing constraints, e.g., removing weeds. If sedge meadows can restore themselves, restorationists will not need to plant sedges or their associated forbs. Steven Hall tested this potential in Gardner Marsh, the former sedge meadow invaded and displaced by hybrid *Typha* as described in Chapter 5—the sedge meadow could not self-restore. In prairie wetlands in northwest Iowa, Karen Kettenring and Dr. Sue Galatowitsch tested the "seed rain" and documented few *Carex* seeds in seed traps. They emphasized that "*Carex* species need to be sown into prairie wetland restorations to overcome dispersal limitations and to preempt the perennial invasive species."

As Steven Hall wrote in 2010, "Ideally, restorationists could eradicate invasive species, and sedge meadows would self-restore." But it's not that simple. In 2006–7, Hall tested three factors that likely constrain self-restoration of sedge meadow: These were depleted soil seed banks, altered hydroperiod, and dominance by *Typha*. He set up experimental plots along the ecotone of the small remnant of sedge meadow being invaded by *Typha:* at a rate of ~0.8 m/year (based on historical aerial photos—see aerial photos in Chapter 5). Random plots were treated in 5 ways, each designed to test an action that should favor sedge meadow self-restoration: (1) harvest and remove all *Typha* ramets; (2) harvest *Typha* a second time, removing regrowth; (3) harvest *Typha* 4 times; (4) herbicide *Typha* using glyphosate; and (5) no-action control. Then, during flooding, he added (6) a one-time harvest of all plants. Note that *Carex* cover was greatest with 4 harvests of the aggressive hybrid *Typha:* but two subplots with 2 harvests also had a strong *Carex* response. In this graph, small a and b indicate within-treatment differences; capital letters identify differences between treatments.



Typha is not easy to remove from a site that has its ideal hydroperiod (stable shallow water) and abundant nutrients. Cutting four times could favor sedges, but what would prevent future re-establishment of *Typha?* The absence of at least 17 forbs from the seed bank of Gardner Marsh indicates that many forbs will not self-restore following removal of *Typha.* Restoration would need to involve preparation of the soil surface, seeding, and transplantation. As shown through Steven Hall's experiments, the longer *Typha* had occupied a site, the fewer *Carex* seedlings emerged from the seed bank. Where *Carex* persisted despite dominance by *Typha,* substantially more *Carex* seedlings emerged. The experiments further showed that *Carex* species and Bluejoint grass (*Calamagrostis canadensis*) emerged and survived only with the drawdown hydroperiod.



Do seed banks persist for decades? The seed bank of a former sedge meadow might retain some of its biodiversity if seeds can persist by avoiding consumption and decomposition and then break dormancy. If so, a species-poor meadow might be able to self-restore. To find out if Gardner Marsh could self-restore, Steven Hall set up a seedling-emergence experiment. He found that seed banks were depleted where *Typha* had eliminated the sedge meadow over a decade earlier (based on aerial photo analysis). His experiment showed that *Carex* and Bluejoint seeds germinated with a drawdown hydroperiod, but a prolonged drawdown was needed for seedlings to survive and persist.

Typha seedlings emerged and survived regardless of hydroperiod—it didn't matter if the water level was fluctuating, flooding, or drawn down. So, loss of sedge dominance can be blamed on the altered hydroperiod (prolonged flooding), depauperate seed banks, and competition with *Typha*. All three factors constrain self-restoration of sedges. Steven Hall and I recommended a long-term management approach that makes use of deep floodwater, namely annually harvesting *Typha* leaf/stem bases below the water level (before or during flood events) at the edges of *Typha* clones, to allow gradual, vegetative self-restoration of *Carex* species. If a site has a water-control structure, this approach is feasible, as the water level can be raised until the *Typha* is smothered.

How do tussocks tolerate variable water levels? Elsewhere, we stressed the importance of restoring natural soil surface forms and heterogeneous topography. We know that *Carex stricta* adds substantial variation to wetland substrates by building tussocks. Beth Lawrence and co-authors (see Chapter 3) concluded that natural *C. stricta* tussocks increase variation in soil moisture and temperature, but what about the reverse? How do tussocks tolerate variable water levels? Our experiments have shown that *C. stricta* plantings can withstand drought, flooding, and alternating flood-dry conditions (in Kercher's mesocosm experiment), as well as a continuous 18 cm water level for 22 weeks (in Lawrence's mesocosm study). Is the tussock the key trait that makes this plant so tolerant of variable water levels? If so, do tall tussocks have greater resilience (ability to persist or recover) than short tussocks?

Kercher's mesocosms

Jim Doherty decided to test effects of tussocks on *Carex stricta* tolerance to variable water levels. With help from volunteers, he created soil mounds of three heights using buckets of wetland soil dumped onto a flat substrate that had been cleared of woody plants to restore a tussock meadow. His experimental mounds were: Small ~8 cm; Medium ~16 cm; Large ~32 cm; and controls with no artificial tussocks. All areas were planted with plugs of *Carex stricta*. Then Mother Nature took over.… Read on.

bucket mounds

In Madison, June is usually the wettest month during the growing season (with ~119 mm of rainfall), but in 2012, June rainfall was only 13 mm, and in 2013, it was 289 mm; these were **record low and high amounts** in the Arboretum's 41-year dataset. Also, daily temperature was higher in 2012 (21.2°C) than in 2013 (17.2°C). These unusual weather conditions were unplanned, but they offered clues to the role of tussocks in tolerating variable environmental conditions. In both years, soil moisture was negatively correlated with elevation (and explained 60% of the variation); thus, some plugs were stressed, as measured by lower cover, biomass, maximum leaf length, and flowering. Overall, 42 of 180 plugs (23%) died during the 2012 and 2013 growing seasons. Most mortalities occurred in drier conditions.

Although it was discouraging to establish an experiment in two successive years with abnormal rainfall, the variable outcomes during environmental extremes made sense and helped explain differential establishment: Tussock sedge grew best on flat ground during the dry spring of 2012 and best on the tall mounds in the wet spring of 2013. Wow—it was a case of **bet-hedging!** Tussock sedge can grow in a wide range of hydroperiods and persist in at least one favorable microsite each year or in each restoration site, thanks to the varied microhabitats of its tussocks. Our results suggest that establishing a diversity of microsites would hedge against suboptimal conditions for establishing plants. And because it is unlikely that any one treatment will guarantee the establishment of a desired species, bet-hedging is a useful strategy, especially for a species that lives

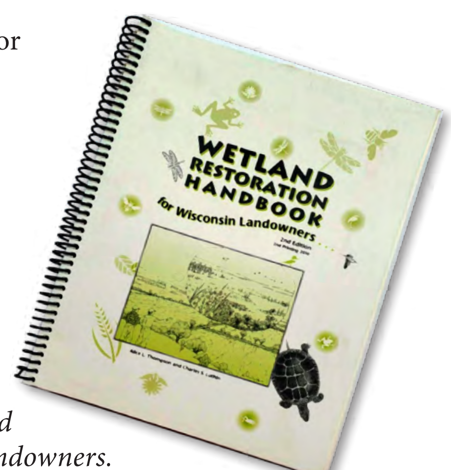
where hydroperiods vary greatly from year to year. Experimentation and bet-hedging are warranted when a wide range of potential conditions can be anticipated.

Looking ahead, Madison can expect extremes, like very dry and very wet conditions in spring, to become more common. It won't be a minor shift in the average rainfall or temperature that causes major dieback of native plant species—at least not in the short term. Instead, it will be *multiple, sudden extremes* that cause severe stress and mortality. Fortunately, Tussock sedge can tolerate high and low water levels during wet and dry years.

Doherty's mounds, top to bottom: Tall, medium, small (flat).

Given the value and services of tussocks, how should we restore sedge meadows?

First, restore wetland hydrology, for example by halting drainage (removing tile systems and blocking drainage ditches, both of which lower the near-surface water table). Readers are encouraged to consult other science-based books. To find potentially restorable wetlands, consult *Wetlands by Design,* which I described above. To select approaches and methods for a site that is potentially restorable, consult Thompson and Luthin's W*etland Restoration Handbook for Wisconsin Landowners.* Both are excellent resources for learning more about where and how to restore wetlands.



Second, we should restore tussock topography because the tussocks are what make *Carex stricta* a **superplant** that can provide nine or more **ecosystem services.** If it takes a decade to develop tussock topography, as it did in northeastern Illinois, then functioning could be augmented by adding mounds early in a project. When done as **large field tests,** restorationists could compare differences among a selection of ecosystem services, e.g., diversity support and resistance to weed invasion.

Bumpy topography will help Tussock sedge survive and grow as the **climate continues to shift** toward more frequent, more intensive rainfall and/or drought. Restorationists can "bet on" multiple microsite types and multiple species or vegetation types. In our plantings, the inclusion of some drought-tolerant prairie species and flood-tolerant emergent species might have increased resilience. Overall, tests of multiple approaches might be the best way to accommodate environmental unpredictability. Opportunities to "learn while restoring" should not be missed.

Jim Doherty's field test suggests that tussock-scale bumps can increase chances of reestablishing Tussock sedge. Besides creating soil mounds, other manipulations might be warranted. The 2012 drought favored an additional planting treatment, namely, placing Tussock sedge plugs in large **peat-pots** that retained moisture better than the soil mounds. Peat pots add cost, so a restoration site could be subdivided to create larger areas with cheaper methods of creating microtopography **(plowing, disking)** plus smaller areas with more labor-intensive work. Volunteers might dig a small depression and pile the shovelful of soil to **make a mound,** thereby providing a wide range of elevations and environmental conditions.

Plugs in peat pots

Third, we should plant natives and control weeds. Where Tussock sedge is absent, it should be planted to help restore its historical, widespread distribution. In southern Wisconsin, a goal could be to re-establish tussock densities that match those of remnant meadows (~4.5 tussocks per m^2). To reduce colonization by invasive plants, monitoring and weed control would be necessary. At the same time, restorationists should reduce factors that diminish tussock heights. These include cattle grazing, fire, and sedimentation.

Summary For Restoring A Tussock Meadow.

Here are several actions for a potentially restorable wetland, such as a former crop field:

Set realistic goals. Expect tussocks to form in sites with prolonged standing water, which encourages rhizomes to grow vertically. Expect lateral growth in sites with brief hydroperiods.

Prepare the site by creating microtopography (e.g. by plowing or disking in larger sites and creating artificial mounds in subsites).

Transplant plugs (units with live roots and shoots; see below) rather than seeds or rhizomes.

Plant plugs in high and low topographic microsites, to hedge against floods/droughts.

Test different spacings for plugs that have rhizomes, e.g., clusters of seedlings at ½ or ¼ the natural density of tussocks ($4\text{-}5/m^2$).

Test soil N levels. A site with N-rich soil should support tussock sedge, but excess nutrients could promote weed invasions.

Be prepared to weed the site frequently in the early stages of restoring a nutrient-rich site.

Remove Reed canary grass, hybrid Cattails and other aggressive invaders, especially those that spread vegetatively.

Engage an army of volunteers. Friends of nature reserves with a mission of biodiversity conservation could potentially sustain a long-term sedge-meadow restoration effort by recruiting an army of volunteers to harvest invasive weeds each year. Remnant sedge meadow vegetation should slowly expand, and native flood-tolerant species could be added to increase sedge meadow diversity.




The army

Very, very tall cattails!

Win-win approaches in Mexico. In Michoacán, Steven Hall and Roberto Lindig-Cisneros learned that local farmers were harvesting the Southern cattail (*Typha domingensis*) up to four times per year to provide fodder for livestock and weaving materials for artisans and crafters. Cattail leaves were being made into baskets, fans, mats, and a myriad of other items for sale to tourists.

Harvested cattail crop

Cattails resprouting

Photos: Steven Hall

Forbs sprouting.

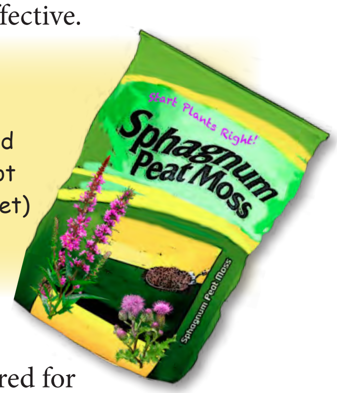
At the same time, harvesting increased species richness in $4 m^2$ plots and whole wetlands. That's a win for people and biodiversity.

Meanwhile, for over a decade, Dr. Lindig-Cisneros had been advocating the management of fire and grazing in Mintzita Springs, which provide drinking water for the capital city of Morelia. Uncontrolled grazing (cattle, horses) and human disturbances were threatening water quality. Then in 2021, the city of Morelia took action to improve water quality, including Cattail removal for handcrafts. A master weaver began teaching locals how to harvest and dry leaves to make saleable items. In another win-win relationship, local artisans now have a new income source while improving surface water quality!

Cattail crafts

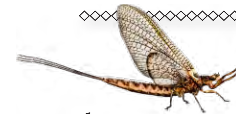
Will the best laid plans always work? No. But we can still learn from attempts that don't achieve their target. For example, peat-extraction sites might be too damaged to restore. Peat is a valuable product in horticulture and gardening, but what happens after the peatland supply is exhausted? After years of extracting peat from European fens, the vegetation cannot recover, and many stripped sites remain bare for decades. A site in Quebec was the first large-scale restoration after commercial-peat extraction in North America. Sphagnum peat had been removed, leaving a sedge peat layer, so the aim was to restore fen vegetation. Water levels were raised by blocking drainage. A nearby donor site provided moss fragments and vascular plant seeds, roots and stems. However, neither the *Carex* species nor a fen community re-established, according to Dr. Line Rochefort, despite trying several methods and waiting five years. A recent review of smaller peatlands was more encouraging. Native plant species in donor sites were present in peat-extraction restoration sites that were >10 years old. More than 80% of the introduced species had established, although *Carex trisperma* and 4 other vascular plants resisted recovery efforts. Lesson? Be prepared to modify the target if restoration efforts are not effective.

CRITICAL THINKING • Check the price of Sphagnum peat that is sold to gardeners online, and calculate what it might cost to replace just a 1-foot layer to restore an acre of land (43,560 square feet) where peat had been extracted



Do animals use disturbed and restored habitats? After a degraded wetland site is prepared for reintroducing vegetation, there's still much to know about how to attract wildlife and which animals might need help getting reestablished.

For many **insects,** the answer is *yes*, they do move into restoration sites. Dragonflies, damselflies, butterflies and moths all are highly mobile and likely to colonize a restored sedge meadow, especially one with diverse forbs that offer pollen and nectar. My long narrow



driveway is wedged between a disturbed wet meadow and a restored prairie, but it attracts diverse butterflies, dragonflies, grasshoppers, and snakes that come and go with the season. It seems that the mowed center of my driveway and the graveled tire tracks offer just what they need for resting, warming, hiding, feeding, and attracting mates. They're also close to tall plants that offer cover when they see me walking to the mailbox.

Above photos: Left, The berm walkway across Waubesa Wetlands offers "edge habitats" between mowed grass and large areas of tall plants; Right, Comma butterfly rests on agravel driveway.

Yes is also the answer for **amphibians.** In Minnesota, Biology Professor Lehtinen at Ohio's Wooster College found 8 species of amphibians that rapidly colonized 5 recently restored wetlands. Restoration consisted of removing drainage infrastructure to allow reflooding. The average number of species per wetland was 3.6. More species re-occupied larger wetlands with suitable habitat and with shorter distances to source populations. Four additional species were found in their 5 reference wetlands. The complete list (12 species) was: *Rana pipiens, R. sylvatica, R. clamitans, Pseudacris triseriata, P. crucifer, Hyla chrysoscelis, H. versicolor, Bufo americanus, B. hemiophrys, Ambystoma tigrinum, A. laterale,* and *Notophthalmus viridescens.*

CRITICAL THINKING • Can you find the common names for each amphibian?

Birds need more study: Habitat preferences need to be known for more sedge meadow birds. Tussock meadows are not usually singled out for studies of birds, but since sedge meadows are often portions of a wetland matrix of marshes and fens, we can assume that the more mobile birds of swamps and marshes could also use sedge meadows.

Sedge wrens (*Cistothorus platensis*) and Marsh wrens (*C. palustris*) nest in coastal wetlands around the Great Lakes, but graduate researcher Hanna Panci and co-authors found that they preferred less-disturbed wetlands. What makes a difference to the selection of home ranges by these wrens? Sedge wrens preferred to nest and forage in emergent herbaceous wetlands, woody wetlands, and sedge meadows **that do not have extensive roads** nearby. Marsh wrens were more tolerant of nearby corn fields and cattail marshes than Sedge wrens. On the whole, the authors recommend limiting development around Great Lakes wetlands to conserve these birds.

In northern Iowa, 19 herbaceous wetlands were restored following cultivation for crops. Prairie potholes (with sedge meadows and shallow-water submerged plants) provided diverse vegetation and diverse foods (especially insects and seeds). While at Iowa State U., Rachel Vanausdall found five breeding birds: Yellowthroat, Swamp sparrow, Marsh wren, and two blackbirds—Red-winged and Yellow-headed.

Slight differences in vegetation separated Marsh wren nesting habitat from that of Red-winged blackbirds, which preferred higher Cattail cover. What might the actual causes be? It seems likely that the structure of the plant canopy would affect the ease of nest construction; some birds might need branched twigs to begin nest building, while others can weave leaves together for the nest base (Red-winged blackbirds in Cattails). Or is the attraction due to preferred prey or less competition from other birds or …? More research is needed.

Raptors find many small animals to prey upon, as well as the young of larger animals. They often leave evidence in the form of a few lost feathers and bits of uneaten prey. In larger sedge meadows, it's common to see Red-tailed hawks soaring overhead, as they are year-round residents; Northern harriers (*Circus cyaneus*) might also be visible as they migrate through the area or stay to nest in large areas with patches of dense vegetation.

Reptiles. Blanding's turtle (*Emydoidea blandingii*) is rare, but I sometimes see an individual crossing a country road as it moves from one wetland to another. Be on the lookout. Watch for a bright yellow neck and dark body.

Snakes are occasionally encountered in the sun on our warm driveway. Luckily for them, "we brake for wildlife." Most sightings are common Gartersnakes (*Thamnophis sirtalis*), which often visit our garage, where the concrete is relatively cool in summer. Milksnakes (*Lampropeltis triangulum*) seem to be more colorful when young, or maybe we have more than one species. Adult snakes help keep the mice in check, since rodents are favorite prey. The Foxsnake (*Pantherophis vulpinus*) has blotches along its back and smaller blotches on its sides. The one I saw was over 4 feet long and looked well fed. I was ok with it sliding under a juniper tree when it noticed

me, even though it meant I couldn't take a photo. They occur across the state in sedge meadows and prairies, and they eat rodents and ground-nesting birds. I'm sure I'll see another before long.

Mammals. Speaking of rodents, there are plenty of Deer mice (*Peromyscus maniculatus*) in and around Waubesa Wetlands. Although their big ears and white underbellies are cute, they can make a mess when they decide to move indoors and build nests! Last year they got into several boxes of holiday ornaments that were stored in a dark closet. When we found them, the wrappings had been converted to fluffy confetti. It reminded me of the pet gerbils I kept in a terrarium as a grad student. At night I gave them each a computer punch card (yes, it was that long ago), and the next morning the terrarium was full of fluff. However, Deer mice are best confined to the outdoors (in their habitat) and viewed at a distance along with Chipmunks (*Tamias striatus*) and Gray squirrels (*Sciurus carolinensis*). Voles (*Microtus* sp.) or other small animals were implicated in a damaged tussock that I found one year; it looked like the animal(s) wanted a place to curl up and hibernate, although the culprit was unknown and escaped apprehension. White-tail deer (*Odocoileus virginianus*) make their rounds daily, and every spring there's a new fawn or twins following behind the doe. Coyote (*Canis latrans*) scat appears on the driveway some mornings, marking their presence the night before. Woodchuck (*Marmota monax*) and

Eastern cottontail (*Sylvilagus floridanus*) disappear into the taller vegetation when they see or hear me. And the ever-present Field mice become more apparent as autumn turns to winter. Tracks and scat are evidence of diverse fauna, despite human disruptions—so long as they are rural lands, not hardscapes.

Grazers: Although deer are native herbivores, they seem to have less impact on tussock meadows than cattle and horses. I am not aware of any evidence that deer graze on Tussock sedge, although their hoof-paths criss-cross the sedge meadows—visible on satellite photos. The short, sharp spikes that persist over the winter would discourage deer browsing between October and early spring. In contrast, Dr. Beth Middleton documented cattle grazing in three sedge meadows near Lodi, Wisconsin. She concluded that cattle grazing likely played a role in the succession of grassy forb meadows

to a **shrub carr** with Red-osier dogwood (*Cornus stolonifera*) as the dominant woody shrub.

If you have the opportunity to volunteer or be paid to help restore a Tussock sedge meadow, you'll learn a great deal and also be able to contribute to a worthy cause. I encourage you to write down your observations, discoveries, and experiences. Scientists can only do part of the work of accumulating information. Practitioners have two roles to play—figuring out how to do restoration well and sharing their knowledge. Who might hire you? Maybe a neighbor with a weed-removal effort or a university student with a research project. Perhaps you could be hired by your local Land Trust or The Nature Conservancy or the Department of Natural Resources. The Society for Ecological Restoration posts jobs on their web site. Good luck!

Did deer or small rodents damage this tussock?

7
How can we grow and manage Tussock sedge?

Tussock sedge is a superplant for restoration in part because it is easy to grow and easy to transplant. Of course, "easy" is a relative term. With information from this book and a little practice, you can learn how and when to collect and germinate seeds, grow seedlings in "conetainers," and transplant plugs to restoration sites. Information on the timing of seed production is in Chapter 3. Here's a how-to guide drawn from the research of Sally Gallagher (Leaflet 22) and papers by Professor Sue Galatowitsch and her students at the University of Minnesota.

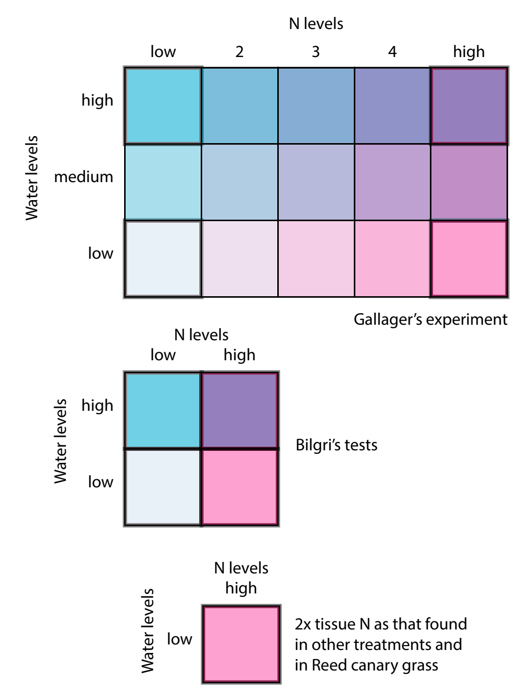
Propagation • Start by growing some "plugs" (small young plants that are easy to poke into the wet soil of a restoration site). You can grow plugs from seeds and then transplant to sites. The tiny seeds will germinate if given warm water and light. You'll recognize germination when a green *epicotyl* emerges (recall that sedges are Monocots).

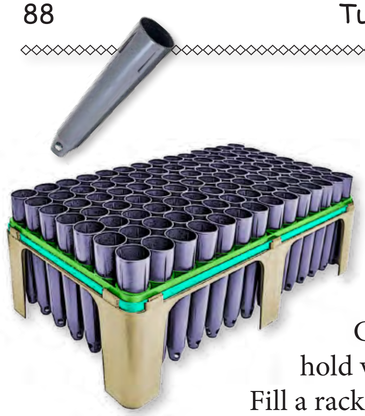
Collect and sprout seeds just before inflorescences shatter and disperse (early June in south-central Wisconsin). Fresh *C. stricta* seeds will germinate without a dormancy period, but if seeds have been stored, rates should be higher if you give them moist or saturated conditions, stored cold (15° C), then germinated with diurnally (day/night) fluctuating temperatures, e.g., 20°/15°C tested in Galatowitsch's lab. Also, *stratification* (cold storage at 22°/8°C or 27°/15°C) for at least 3 months caused seeds to germinate more rapidly in Minnesota tests by doctoral student Kettenring and Dr. Galatowitsch. These authors also found that *C. stricta* seed germination was highest with 35°/30°C day/night temperatures. I have germinated hundreds of Tussock sedge seeds outdoors in warm, sunny conditions by placing seeds in black trays with very shallow water in full sun. Watch and water them daily and count the green epicotyls.

What is the adaptive value of the need for such a high temperature to stimulate germination? Adaptive value comes from high survival rates. Here's one idea: In a sedge meadow, I saw abundant Tussock sedge seedlings from seeds that germinated on black (and thus very warm) organic soil exposed to full sun. A seed that waits for a canopy opening is more likely to establish a seedling than one that might germinate in cooler shade and not have enough light to grow well. Doctoral student Roberto Lindig-Cisneros showed this effect on Reed canary grass seeds—they remained dormant under a dense canopy but began germinating as soon as Roberto cut 10x10cm openings in the overstory.

For her M.S. thesis research, Sally Gallagher worked out ways to grow seedlings in outdoor microcosms (1-gallon buckets) at the Arboretum. There, she subjected plugs to three water levels and 5 nitrogen (N) levels, for a total of 15 treatments. Student Alex Bilgri took advantage of her experiment for his senior thesis: He analyzed tissue-N content of roots, rhizomes, leaf bases, and leaves from Sally's highest and lowest levels of nitrogen and the highest and lowest water levels. At 4 months, plants grown with high N + low water reached maturity and had the greatest nitrogen concentration (~9–10mg N/g) in all four tissues. This was twice the tissue-nitrogen found in high N + high water, low N + low water, and low N + high water treatments. Bilgri noticed that this was also twice as much tissue-N as in the highly invasive Reed canary grass, analyzed by doctoral student Andrea Herr-Turoff.

More recently, Professor Scott Holaday's lab in Texas showed that Reed canary grass is indeed more efficient at taking up and using nitrogen.





Sally Gallagher advised growing Tussock sedge as follows: Remove the germinating seeds with fine tweezers and place each in its own conetainer that you've filled with potting soil. Garden shops should have racks that hold various numbers of "conetainers." Fill a rack of conetainers and place it in a deep pan with enough water to keep the soil saturated. Conetainers work well as individual planting units (plugs). This is consistent with the advice of graduate student Rachel Budelsky and Dr. Sue Galatowitsch, namely, to grow seedlings and plant them as plugs rather than transplanting bare-root rhizomes. The first growing season is critical; thereafter, plants can tolerate more flooding and drying, as well as resist competition from annual and perennial weeds—except for Reed canary grass. Follow Sally Gallagher's guidelines—when seedlings are growing, add nitrogen (N) to tailor growth as needed:

–to conserve greenhouse space and hold plugs until the planting site is ready, *withhold* N and keep the water level below the soil surface.

–to accelerate shoot growth, *add* N.

–to enhance vegetative spread, add N to plugs and keep the soil saturated.

–to produce rhizomes, grow seedlings for at least two seasons. Plugs with obvious adventitious roots (arising above the soil) should begin to form tussocks in their second year if grown in shallow standing water (with leaves exposed to air and sunlight).

Burning • Is fire management really necessary? According to Milo Coladonato at the USDA Forest Service, *Carex stricta* is "resistant to fires that *burn little* of the soil organic layer" and that fire is "important to the maintenance of the sedge meadow community" by preventing "encroachment of shrubs and trees." While wet conditions protect belowground roots and rhizomes, fire is damaging during severe droughts and in drained meadows. If the peat ignites, it can smolder belowground for weeks and destroy roots and rhizomes. As the surface

elevation becomes lower and water levels rise, the sedge meadow might convert to a Cattail marsh.

Tussocks are living, organic structures with a solid pedestal that is up to 95% organic, plus a cloak of leaves. They burn when dry and ignited. Still, some land managers like to burn sedge meadows to deter woody plant invasions. Is it really necessary to burn, or can it do more harm than good? Here are both pros and cons:

Reasons to burn

- Woody plant invasions might be reduced.
- Fire releases nutrients, which could increase the first season's growth and/or flowering.
- Native species' seeds might be stimulated to germinate.

Reasons not to burn tussocks

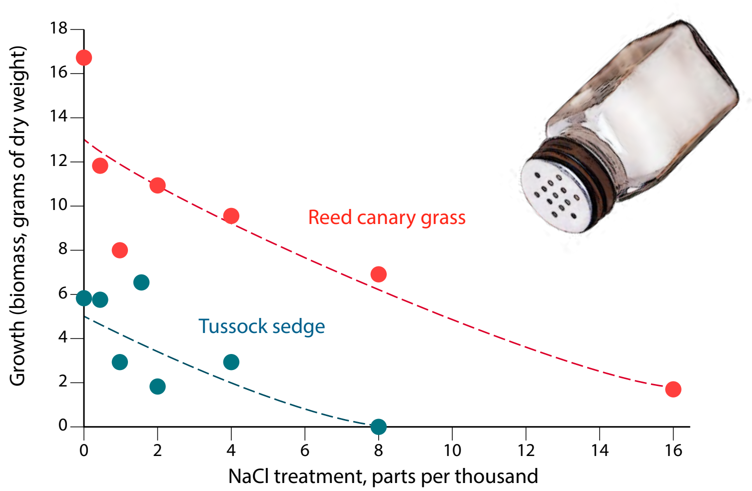
- Tussocks grow slowly with infrequent inundation and more rapidly in wetter hydroperiods. It might take a decade to grow just 15 cm tall.
- Compared to short tussocks, tall tussocks grow longer leaves, produce more inflorescences more frequently, and persist in the face of disturbances from humans and wildlife
- The tussock retains senesced leaves from the previous growing season and some from previous years, plus decomposing litter. Fire consumes the loose material and some unknown fraction of the solid structure.

Southern Wisconsin sedge meadow after a control burn followed by snowfall.

- Fire releases stored C to the atmosphere.
- In spring, spikes that have overwintered emerge early and gain an advantage in early growth. Burning would likely "cook" the spikes. Regrowth will take extra time.
- Seeds of invaders, like Reed canary grass and Cattails, are stimulated to germinate on exposed substrates.
- Invaders can take advantage of nutrients that are released.
- The habitat of Voles and other native animals that live in and under tussocks would be disrupted.
- Tussocks are vulnerable to other disturbances such as Deer trampling/bedding, which we cannot control; unnecessarily burning "old growth" tussocks adds to other threats.
- Tussock meadows are greatly diminished due to drainage and conversion to other land uses; the remaining tussock meadows deserve protection and science-based management.

Where there are unknowns and uncertainties, there is a need for research. I recommend not burning unless research clearly shows that hypothesized benefits of fire exceed detrimental impacts.

Avoid use of salt that can flow into sedge meadows.



When you find a plant growing in saline soil, you know it's salt tolerant. But a sedge that has never been exposed to saline soil will be harmed by runoff from salted streets and roads. Road salt will

very likely damage *Carex* species. Student Nick Prasser tested salt tolerance of Tussock sedge for his senior thesis at UW–Madison. The results warranted publication. Compared to our state's worst wetland weed, Reed canary grass, our native *C. stricta* could not grow at all at 8 ppt (parts per thousand = grams per liter) of salt (NaCl), and it could grow only slowly at 4 ppt. Meanwhile, Reed canary grass could still grow at 16 ppt, which is half the salt concentration of sea water.

CRITICAL THINKING • In a roadside ditch that receives Wisconsin snow meltwater, and where both Reed canary grass and Tussock sedge are present, which will have the competitive advantage, native Tussock sedge or alien Reed canary grass?

8
Why should we protect all the values of wetlands?

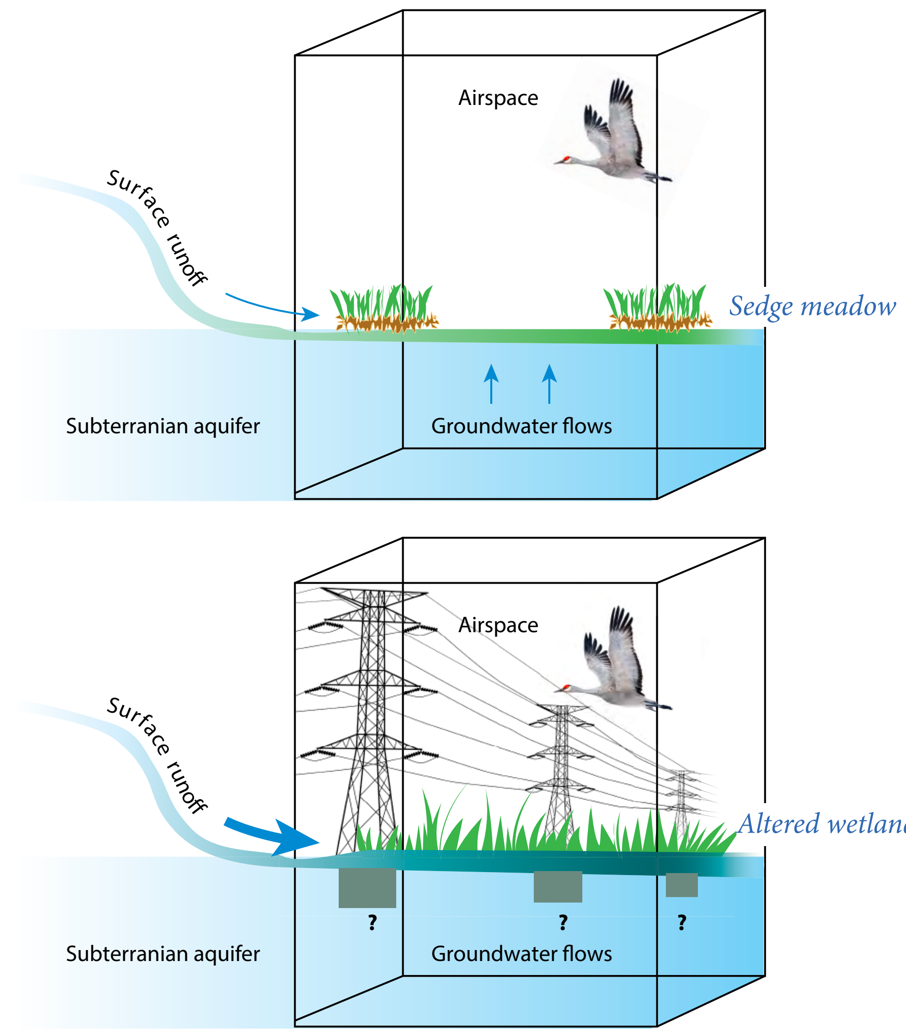
Wetlands are 3-Dimensional ecosystems. Human activities have impacts on all parts of ecosystems, but our impacts on the vertical components (above and below the ground) can be especially harmful. Below the ground, it's because the water levels and water quality are often the critical factors for sustaining biodiversity and functions. And above the ground, thousands of migratory birds can be damaged by powerlines that obstruct their flight pathways. While wetlands might appear to be flat, they are much more than meets the eye. What you see on the ground is only a fraction of what makes up a wetland.

Aboveground, wetlands offer flight pathways and landing pads for insects, birds, and bats 24/7. Because wetlands attract and support millions of water birds, their air space needs to be protected. Powerlines add tall structures around and in wetlands. While powerline proponents claim that cluttered airspace has no significant impact, a flight path that looks like open space can be lethal to birds attempting to fly through "openings." And birds that try to land in wetlands can be ensnared by wires that connect towers. Birds that fly in the daytime might be able to avoid powerlines, but those that fly in dim light are more vulnerable. North-south migrants would find it hard to avoid crossing an east-west powerline. Birds that migrate every fall and spring don't need more obstructions.

On the ground, powerline rights-of-way are cleared of trees and mowed, which changes upland ecosystems and invites weeds. Electric lines cause wildfires and, in hilly topography, the removal of trees causes more surface water to flow downslope, carrying more soil and nutrients into flat spaces and their wetlands. The addition of nutrients to wetlands encourages weeds and discourages native species.

Belowground, it might seem that plunking a power tower in a wetland has no effect. But the tower foundations interfere with flows of groundwater, as do berms that connect towers for access by maintenance crews. Massive concrete bases displace native plants and animals—and reduce the wetland's ability to soak up flood waters, purify runoff, and store carbon in the soil. It doesn't take

much of a change in water flow and depth (hydroperiod) to shift a species-rich wetland to a weedy patch of alien Cattails. Such shifts are aided by soil disturbance during construction. Even a 6-inch pile of dirt invites weedy shrubs and trees to invade a wet meadow or marsh. Wetlands don't take kindly to altered hydroperiods.



Wetlands encounter threats belowground, on the surface, and aboveground.

Powerline across the wetlands south of Lake Waubesa

Damages to wetlands can seem to be temporary, ending when the bulldozers leave and the wounds become covered by something green. But altered ecosystem structures and functions persist long-term, above- and belowground. The powerline that dissects Waubesa Wetlands (at the toe of Lake Waubesa) is not just an eyesore. It has weedy vegetation surrounding every tower placed in wetland soil and more weeds along the linear berm. Powerlines challenge the ability of native species to persist in an ever-more-altered, human-dominated Earth.

Courtesy of the Aldo Leopold Foundation and University of Wisconsin-Madison Archives

Early conservationists, notably Aldo Leopold, argued against exploiting natural resources to the maximum. We can reduce our waste of electrical power and harness greener sources of energy. It is in our own best interest to protect wetlands for their 3-D support of biodiversity and human well-being. Leopold's words have gained importance over time, as powerlines and other tall structures stretch across urban landscapes and the corridors between them.

If restorationists add heterogeneous topography to restoration sites, there will be more varied micro-sites to support diverse species and jump-start tussock formation. And if they introduce diverse plantings with both drought- and flood-tolerant species, the vegetation will be able to hedge bets against extreme conditions.

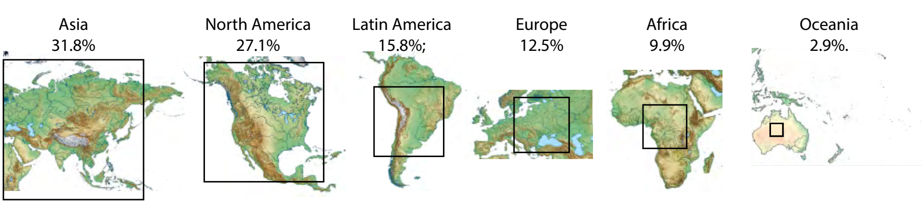
8

Let's protect wetlands for their services and our well-being!

If we don't damage our native wetlands, we won't need to restore them. It is always wiser preserve what is valued than to lose it and try to replace it. Tussock meadows should be conserved to stabilize and reverse the trend of diminishing wetland area, as well as to sustain species richness and a multitude of ecosystem services. The Nation's wetlands are **disproportionately important** to human well-being. That means their area is small relative to the services they provide. In 2018, Australian Professor Davidson and co-authors estimated that wetlands contribute ~43.5% of the ecosystem services of all natural biomes. This is amazing, given the small area (< 9%) of the Earth that is wetland.

First, how much area do wetlands occupy? The number of square km is based on high-resolution aerial imagery: 12.1 million square kilometers. Of the global total, nearly all the areas are inland wetlands (92.8%) and ~2% of that is coastal. Some 54% of wetland area is permanently inundated and thus not sedge meadow. The remaining 46% is temporarily inundated; that includes sedge meadows.

Where are most of Earth's wetlands? The greatest proportion is in the north hemisphere: Asia has 31.8% of the total, North America has 27.1%; and Europe has 12.5%. Further south, where wetlands are less well mapped, Latin America and the Caribbean have 15.8%; Africa has 9.9% and Oceania has 2.9%. The northern hemisphere has more wetland area as well as more total land area.



Boxes indicate relative % of Earth's wetland areas

As a review, key services of tussock meadows are:

- **Supporting biodiversity**
- **Storing carbon**
- **Reducing flooding**
- **Cleaning stormwater runoff**
- **Removing excess nitrogen**
- **Oxidizing methane**
- **Fixing nitrogen if limiting**
- **Providing useful materials**
- **Supporting wildlife**

To these functions, we can add a wealth of **cultural services,** including Nature appreciation (e.g., bird watching), open space (pleasant places to enjoy views), solitude (an escape from the stresses of modern society). and inspiration (for art, poetry, and books, such as this one).

The ecosystem services of tussock meadows are especially impressive, considering that they are dominated by a mild-mannered, herbaceous plant. I say "mild-mannered," because Tussock sedge is not a giant tree that can form a forest or a woody shrub whose tangled branches can block our paths, or a broad-leaved bully that easily grabs all the light. It's an herbaceous sedge that has what might be considered serious constraints—narrow leaves that emerge, grow and die over the summer growing season, turning to litter that might form peat or simply decay; flowers without petals that rely on the wind for pollination; tiny fruits and seeds that mostly remain dormant because the sedge reproduces primarily by sending rhizomes laterally to expand its clump or vertically to elevate its tussocks—slowly but surely. It's a mild-mannered **superplant.**

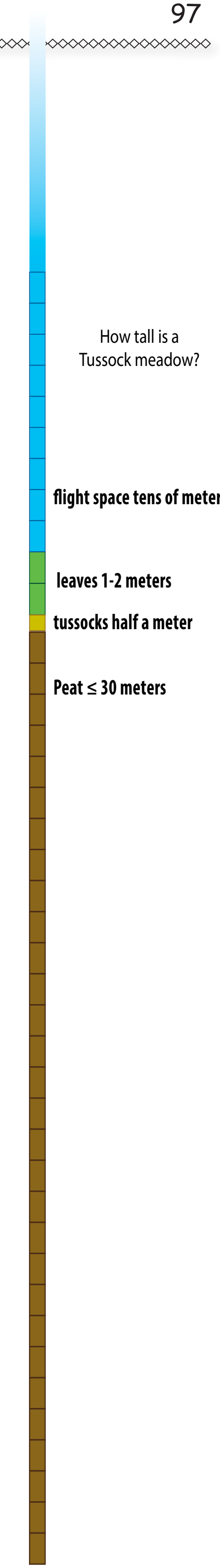
The tussocks are the key to Tussock sedge's persistence and dominance. Tussocks elevate the growing points (leaf bases) above spring floodwaters. They support processes that rely on both aeration (oxic conditions that allow methane oxidation) and stagnation (anoxic conditions, facilitating denitrification and peat formation). Whereas the leaves are ephemeral, the tussocks are long-lived, packed with rhizomes, and rich in stored carbon.

Collectively, the tussocks reshape wetland surfaces, adding a rough estimate of up to 40% in total surface area for all those ecosystem services to take place. Not bad for a modest plant!

How can we help tussock meadows persist into an uncertain future?

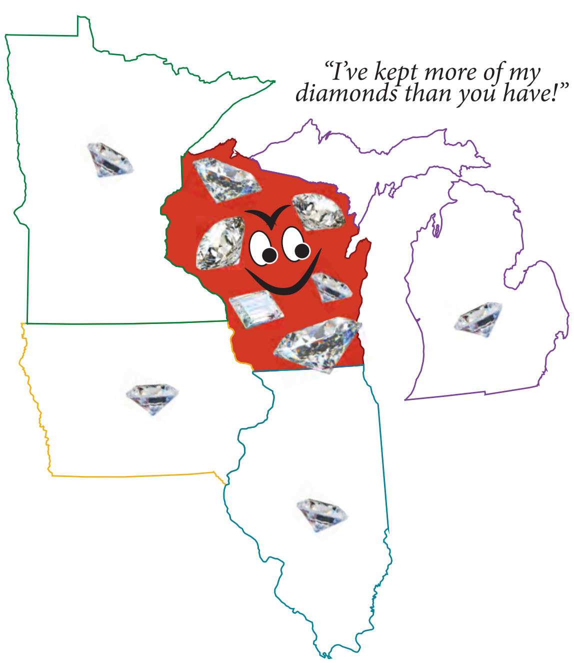
First, let's recognize the importance of all **three dimensions** of tussock meadows and manage them accordingly.

Tussock meadows are more than what meets the eye. What we see is only a fraction of the ecosystem. On the ground, the tussocks and their canopy of leaves are 1-2 meters tall during the height of the growing season. Unseen, however, are the belowground portions of the tussocks, which extend perhaps a third or half a meter into the wetland soil, while their peat deposits that have accumulated over decades to centuries might be one to several meters deep (Waubesa Wetlands have peat that Professor Cal DeWitt measured as over 30 meters deep). Above the sedge canopy, small birds make daily use of the vertical dimension of the ecosystem by several meters. And Sandhill cranes and other birds that take off to fly overhead—or fly in to land—extend the third dimension to tens of meters above the sedge canopy. Thus, any unnatural structures, on the ground, below the ground, or in the flight path will intrude on the tussock meadow ecosystem. Wetland functions can be greatly underestimated if we only consider them in 2-D. What we can see on the ground is connected to what happens below and above the ground, as well as within and beyond the wetland

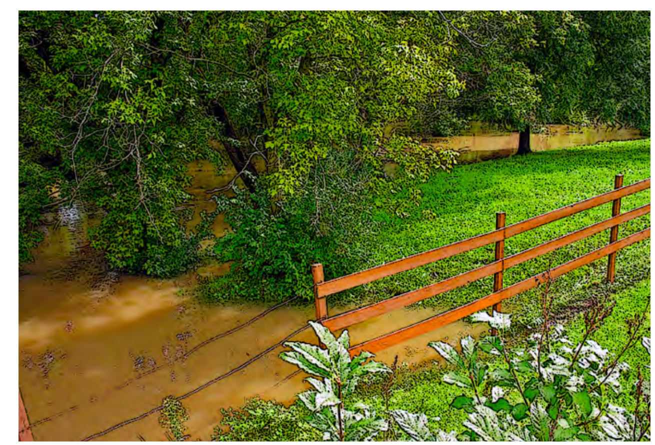


Second, let's emphasize the **dynamics** of tussock meadows and find ways to make them be more **resilient** to rapid environmental shifts associated with our changing climate. Resilient means able to **resist** impacts and/or **recover** from impacts. The climate is changing rapidly, so how can researchers separate short-term variations from extremes when we don't know how long an unusual event will persist? Above, Jim Doherty and I called for *bet hedging* to **enhance the resilience** of ecosystems.

Summary: Wetlands are like diamonds — small but extremely valuable. As stated earlier, Wisconsin had lost 46% of its wetland area by 1980 (see report by Tom Dahl). That total comes from many wetlands that were completely destroyed and many that were shrunk around the edges or dissected by roads. Still, Wisconsin retained 54% of its 1780s wetland area, while neighboring states to the south and east retained only ~15% of their historical wetland area. Wisconsin treasures its sedge meadows, fens, woodland swamps and marshes. They are not just pretty places and rare gems; they support much of the rest of Nature and human well-being. Jim Doherty pointed out that diamonds and wetlands are also alike in having lesser-known uses. Diamonds provide industrial abrasives (tiny but extremely hard particles); they are critical in polishing and finishing operations. Tussock meadows are not well known for abating global warming, but their tussocks can be critical in oxidizing methane, a potent greenhouse gas! Jim called Tussock sedge "a quiet biogeochemical workhorse." I agree!



Here's what wetlands are doing for me today: Wetlands are busy cleaning up muddy stormwater runoff after heavy rainfalls. On Aug. 20, 2018, the Madison area received record rainfall for a 24-hour period, and local lake levels rose to the 100-year-flood mark. Did you notice the brown water in the street gutters, creeks and streams? It was carrying soil that washed off fields and construction sites, and it picked up nutrients and contaminants on its way to downstream wetlands and lakes. Due to health threats, all Madison-area beaches were closed. Except during major storm flows, wetlands have time to make turbid water clear by removing pollutants—things we cannot see, including nitrogen and phosphorus that feed algal blooms, toxic heavy metals and pesticides that poison our surface waters, and germs that can cause diseases. Some of these pollutants are being soaked up by wetlands, and some are being denatured by friendly wetland microbes.



Swan Creek flood

Thanks to wetlands, our lakes and beaches can be safe, sooner than without wetlands. And just by collecting water, wetlands are reducing floods, slowing surface water, and keeping basements drier than they might be without upstream wetlands. In between storms, wetlands produce tons of food for wildlife and waterbirds, provide habitats that support diverse plants and animals, and feed larval fish until juveniles grow big enough to move into the adjacent lake where anglers can harvest the marsh nursery's bounty. And wetlands serve all who enjoy nature by sight-seeing, photographing, sketching, hiking and canoeing. And there's more. Just by being wet, the soil becomes anoxic and the organic matter decomposes very slowly. As a result, carbon-containing materials accumulate as peat, and the more carbon stored in peat the less carbon escapes as greenhouse gas. Without peat-forming wetlands, the Earth would be even warmer, with more big storms. Wetland soils also denature nitrogen, returning human-made fertilizers back to the air as harmless nitrogen gas. Without upstream wetlands busily removing nitrogen, the Gulf of Mexico would have an even bigger **dead zone** and the price of shrimp would skyrocket. How does that follow?

Follow the chain of impact

N fertilizer in the
Mississippi River watershed

↓

N flows into Gulf of Mexico

↓

Algae "bloom" in surface water

Dense algae shade the sub-surface water

↓

Less photosynthesis, more cells die
More decomposition

Less oxygen in the water column

↓

Dead zone
for invertebrates and fishes

↓

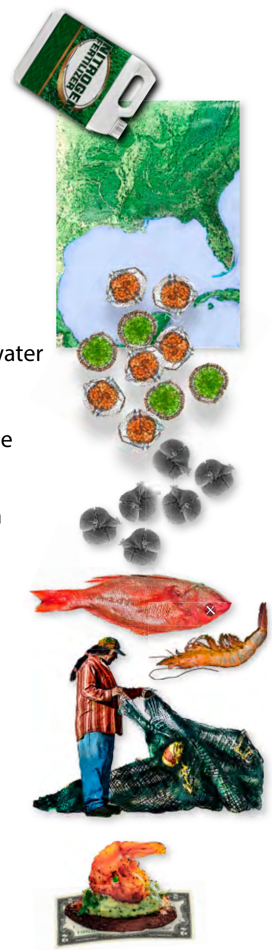
Fishers can't catch any seafood

↓

Seafood supply declines

↓

Shrimp costs more



Think of wetlands as being worth their weight in diamonds. As discussed earlier, a recent estimate is that global wetlands provide over $47 trillion per year worth of services such as cleaning surface water, storing carbon, abating floods, supporting food webs that supply fish, maintaining biodiversity, offering recreation, and inspiring people!

Inland freshwater wetland services are estimated to be worth about *$10,500 per acre per year* in calculations by Dr. Robert Costanza and collaborators. Wetland benefits are great reasons to protect those that remain and to restore more of what has been drained or filled. Wetlands might be small, relative to uplands and deep waters. But like diamonds, they are extremely valuable and deserving of our utmost care.

10
Suggestions for further reading

Where can curious readers find more information? Here are references to consult in relation to each chapter. The standard format for scientific articles is:

Author or authors • Year of publication • Title of article • Journal name • Volume number (Issue number): Pages in the journal • Doi. The Doi is a unique Digital Object Identifier; use it to search for a paper online. Not all papers are posted on the web; some journals retail copyrights. Finding sources of information is becoming easier; at the same time, the literature available grows faster every year!

Note that several papers are relevant to two or more chapters, so there is some repetition in the lists. The lists include many papers published at UW–Madison, since this book focuses on the work of my students and other collaborators. —JZ

Chapter 1 • What's Unique About Sedges?

Christenhusz MJM, Fay MF, Chase MW. 2017. Plants of the World: An Illustrated Encyclopedia of Vascular Plants. Kew Publishing, Royal Botanic Gardens, Kew, England, UK.

Hipp A. 2008. Field Guide to Wisconsin Sedges: An Introduction to the Genus *Carex* (Cyperaceae). University of Wisconsin Press, Madison.

Stevens ML. 2020. Eco-cultural restoration of riparian wetlands in California: Case study of White root (*Carex barbarae* Dewey; Cy peraceae). Wetlands 40: 2461–2475. Doi.org/10.1007/s13157-020-01323-3.

Chapter-2 • Is There A Special Wetland Sedge?

Bedford BL, Zimmerman EH, Zimmerman JH. 1974. The Wetlands of Dane County, Wisconsin. Dane County Regional Planning Commission, with WI Department of Natural Resources. Madison.

Budelsky RA, Galatowitsch SM. 1999. Effects of moisture, temperature, and time on seed germination of five wetland *Carices:* Implications for restoration. Restoration Ecology 7: 86–97.

Budelsky RA, Galatowitsch SM. 2004. Establishment of *Carex stricta* Lam. seedlings in experimental wetlands with implications for restoration. Plant Ecology 175: 91–105.

Costello DF. 1936. Tussock meadows in southeastern Wisconsin. Botanical Gazette 97: 610–648.

Frieswyk CB, Johnston C, Zedler JB. 2007. Identifying and characterizing dominant plants as an indicator of community condition. Journal of Great Lakes Research 33(Special Issue 3):125-135. Hall SJ, Zedler JB. 2010. Constraints on sedge meadow self-restoration in urban wetlands. Restoration Ecology 5: 671-680.

Hipp, A. 2008. Field Guide to Wisconsin sedges: An introduction to the genus *Carex* (Cyperaceae). University of Wisconsin Press, Madison.

Leaflet 22. 2010. Tussock sedge–A restoration superplant? Zedler JB. Online, Arboretum, University of Wisconsin, Madison.

McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin A, Kjelland K, Bonnie L, Kwiatkowski BL, Laundre JA, Murray G. 2002. Resource-based niches provide a basis for plant species diversity and dominance in Arctic tundra. Nature 415: 68-71.

Wenthe A. 2017. Restoring a wetland gem: Applications of current tools and technologies at Waubesa Wetlands State Natural Area. M.S. Report, Botany Department. University of Wisconsin-Madison.

Woo I, Zedler JB. 2002. Can nutrients alone shift a sedge meadow towards the invasive *Typha* x *glauca*? Wetlands 22: 509-521.

Chapter 3 • How Does Tussock Sedge Grow Year After Year?

Bernard JM. 1990. Life history and vegetative reproduction in *Carex*. Canadian Journal of Botany 68:1441-1448.

Costello DF. 1936. Tussock meadows in southeastern Wisconsin. Botanical Gazette 97: 610–648.

He, Z, Bentley LP, Holaday AS. 2011. Greater seasonal carbon gain across a broad temperature range contributes to the invasive potential of *Phalaris arundinacea* L. (Poaceae, reed canary grass) over the native sedge, *Carex stricta* LAM. (Cyperaceae). American Journal of Botany 98: 20-30.

Zedler JB. 2016. Phenology of *Carex stricta:* It pays to be tall! Wetland Science & Practice 33(1): 14-21. https://issuu.com/societyofwetlandscientists/docs/march_2016_wsp.

Ch 4 • What Makes Tussock Sedge A "Superplant"?

Costanza R, dArge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S., Oneill, RV, Paruelo J, Raskin RG, Sutton P, van den Belt M., 1997. The value of the world's ecosystem services and natural capital. Nature 387 (6630), 253–260.

Costanza R, de Groot R, Braat L, Kubiszewski I, Fioramonti L, Sutton P, Farber S, Grasso M. 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosystem Services 28: 1–16.

Eckardt NA, Biesboer DD. 1988. Ecological aspects of nitrogen fixation (acetylene reduction) associated with plants of a Minnesota wetland community. Canadian Journal of Botany 66: 1359-1363. Doi.10.1139/b88-190.

Frieswyk CB, Johnston C, Zedler JB. 2007. Identifying and characterizing dominant plants as an indicator of community condition. Journal of Great Lakes Research 33(Special Issue 3):125-135.

Haase D. 2017. Urban wetlands and riparian forests as a nature-based solution for climate change adaptation in cities and their surroundings. In: Kabisch N, Korn H., Stadler J, Bonn A. Editors. Nature-Based Solutions to Climate Change Adaptation in Urban Areas. Theory and Practice of Urban Sustainability Transitions. Springer. Doi.org/10.1007/978-3-319-56091-5_7.

Hall SJ. 2004. Topographic heterogeneity increased species richness in a wetland restoration. Botany Senior Thesis. U. Wisconsin, Madison, WI.

Hugron S, Guene-Nanchen M, Roux N, LeBlanc M-C, Rochefort L. 2020. Plant reintroduction in restored peatlands: 80% successfully transferred—Does the remaining 20% matter? Global Ecology and Conservation 22, e01000, ISSN 2351-9894

Jitka V, Jiri D, Stanislav S, Lenka M, Hana C. 2017. Effect of hummock-forming vegetation on methane emissions from a temperate sedge-grass marsh. Wetlands 37: 675-686.

Johnston CA, Zedler JB. 2012. Identifying preferential associates to initiate restoration plantings. Restoration Ecology 20: 764-772.

Land M, Granéli W, Grimvall A, Hoffmann CC, Mitsch WJ, Tonderski KS, Verhoeven JTA. 2016. How effective are created or restored freshwater wetlands for nitrogen and phosphorus removal? A systematic review. Environmental Evidence 5, 9. doi.org/10.1186/s13750-016-0060-0.

Larkin D, Bruland G, Zedler JB. 2016. Chapter 10, Heterogeneity theory and ecological restoration. *In:* Palmer M, Zedler JB, Falk D. 2016. Foundations of Restoration Ecology, 2nd Edition. Island Press, Washington, DC.

Lawrence, BA, Zedler JB. 2011. Formation of tussocks in sedges: Effects of hydroperiod and nutrients. Ecological Applications 21: 1745-1759.

Lawrence BA, Zedler JB. 2013. Carbon storage by *Carex stricta* tussocks: A restorable ecosystem service? Wetlands 33:483-493.

Lawrence BA, Fahey T, Zedler JB. 2013. Root dynamics of *Carex stricta*-dominated tussock meadows. Plant and Soil 364: 325-339. Doi.10.1007/s11104-012-1360-y.

Lord LA. 1996. Competition and dispersal in the regulation of plant species richness on *Carex stricta* tussocks. Ph.D. Dissertation, University of New Hampshire, Durham, NH.

Lord LA, Lee TD. 2007. Interactions of local and regional processes: Species richness in tussock sedge communities. Ecology 82: 313–318.

McKown JG, Moore GE, Payne AR, White NA, Gibson JL. 2021. Successional dynamics of a 35-year-old freshwater mitigation wetland in southeastern New Hampshire. PLoS ONE. May 17, 2021. Doi.org/10.1371/journal.pone.0251748.

Middleton B. 2002. Nonequilibrium dynamics of sedge meadows grazed by cattle in southern Wisconsin. Plant Ecology 161: 89-110.

Ouyang Z, Song C, Zheng H, Polasky S, Xia Y, Bateman IJ, Liu J, Ruckelshaus M, Shi F, Xiao Y, Xu W, Zou Z, and Daily GJ. 2020. Using gross ecosystem product (GEP) to value nature in decision making. Proceedings of the National Academy of Science 117(125): 14593-14601.

Peach MA, Zedler JB. 2006. How tussocks structure sedge meadow vegetation. Wetlands 26: 322-335.

Perelman, SB, Burkart SE, León RJC. 2003. The role of a native tussock grass (*Paspalum quadrifarium* Lam). in structuring plant communities in the Flooding Pampa grasslands, Argentina. Biodiversity and Conservation 12: 225-238.

Rejmánková E, Sirová D, Castle ST, Bárta J, Carpenter H. 2018. Heterotrophic N2-fixation contributes to nitrogen economy of a common wetland sedge, *Schoenoplectus californicus*. PLoS ONE 13(4): e0195570. Doi. org/10.1371/journal.pone.0195570.

Stevens ML. 2020. Eco-cultural restoration of riparian wetlands in California: Case study of White root (*Carex barbarae* Dewey; Cyperaceae). Wetlands 40: 2461–2475. Doi .org/10.1007/s13157-020-01323-3.

Vanausdall RA, Dinsmore SJ. 2020. Detection and density of breeding marsh birds in Iowa wetlands. PLoS ONE 15(1): e0227825. Doi.org/10.1371/journal.pone.0227825

Watson KB, Ricketts T, Galford G, Polasky S, O'Niel-Dunne J. 2016. Quantifying flood mitigation services: The economic value of Otter Creek wetlands and floodplains to Middlebury, Vermont. Ecological Economics 130: 16–24.

Wang M, Wang G, Wang S, Jiang M. 2018. Structure and richness of *Carex meyeriana* tussocks in peatlands of Northeastern China. Wetlands 38: 15–23.

Werner KJ, Zedler JB. 2002. How sedge meadow soils, microtopography, and vegetation respond to sedimentation. Wetlands 22: 451–466.

Whisenant S. 1999. Repairing Damaged Wildlands: A Process-Oriented Landscape-Scale Approach, Cambridge University Press, Cambridge, UK.

Wickstrom CE, Gorano J. 2007. Associative rhizosphere nitrogen fixation (acetylene reduction) among plants from Ohio peatlands. Ohio Journal of Science 107: 39-43.

Wolf K, Ahn C, Noe G. 2011. Microtopography enhances nitrogen cycling and removal in created mitigation wetlands. Ecological Engineering 37: 1398–1406.

Woltemade CJ. 2000. Ability of restored wetlands to reduce nitrogen and phosphorus concentrations in agricultural drainage water. Journal of Soil and Water Conservation. Third Quarter 303-309.

Yu F-H, Krüsi B, Schütz M, Schneller J, Wildi O. 2006. Is vegetation inside *Carex sempervirens* tussocks highly specific or an image of the surrounding vegetation? Journal of Vegetation Science 17: 567-576.

Chapter 5 • When And Why Were So Many Wetlands Lost?

Biebighauser TR. 2007. Wetland Drainage, Restoration, and Repair. University Press of Kentucky, Lexington, KY.

Boers A, Zedler JB. 2008. Stabilized water levels and *Typha* invasiveness. Wetlands 28: 676-685.

Carpenter Q. 1995. Toward a new definition of calcareous fen. Ph.D. Dissertation. U. Wisconsin, Madison, WI.

Curtis JT. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison.

Dahl T. 1990. Wetlands losses in the United States 1780s to 1980s. Department of the Interior, US Fish and Wildlife Service, Washington, DC.

Frolik AL. 1941. Vegetation on the peat lands of Dane County, Wisconsin. Ecological Monographs 11(1): 117-140.

Hall SJ, Zedler JB. 2010. Constraints on sedge meadow self-restoration in urban wetlands. Restoration Ecology 5: 671-680.

Irwin H. 1973. A natural history study of East Marsh of the University of Wisconsin Arboretum. M.S. Thesis, University of Wisconsin, Madison, WI.

Larkin D, Lishawa J, Tuchman N. 2012. Appropriation of nitrogen by the invasive Cattail *Typha* x *glauca*. Aquatic Botany 100: 60-66.

Leaflet 17. 2008. Demystifying fens. Carpenter Q, Zedler JB. Online, Arboretum, University of Wisconsin, Madison, WI.

Lindig-Cisneros R, Zedler JB. 2002. *Phalaris arundinacea* L. seedling establishment: Effects of canopy complexity in fen, mesocosm and restoration experiments. Canadian Journal of Botany 80: 617-624.

Owen C. 1999. Hydrology and history: Land use changes and ecological responses in an urban wetland. Wetlands Ecology and Management 6: 209–219.

Woo I, Zedler JB. 2002. Can nutrients alone shift a sedge meadow towards the invasive *Typha* x *glauca?* Wetlands 22: 509-521.

Zedler JB, Potter K. 2008. Southern Wisconsin's herbaceous wetlands: Their recent history and precarious future. Pages 193-210 in The Vanishing Present. Waller D, Rooney T. Editors. University of Chicago Press, Chicago, IL.

Chapter 6 • How Can We Restore Tussock Meadows?

Ding H, Faruqi S, Wu A, Altamirano J-C, Ortega AA, Zamora-Cristales R, Chazdon R, Vergara W, Verdone J. 2018. Roots of Prosperity: The Economics and Finance of Restoring Land. World Resources Institute, Washington, DC.

Doherty JM, Zedler JB. 2015. Increasing substrate heterogeneity as a bet-hedging strategy for restoring wetland vegetation. Restoration Ecology 23: 15-25. Doi: 10.1111/rec.12154.

Frieswyk CB, Johnston C, Zedler JB. 2007. Identifying and characterizing dominant plants as an indicator of community condition. Journal of Great Lakes Research 33(Special Issue 3):125-135.

Frieswyk CB, Zedler JB. 2006. Do seed banks confer resilience to coastal wetlands invaded by *Typha* x *glauca?* Canadian Journal of Botany 84:1882-1893.

Galatowitsch SM. 2012. Ecological Restoration. Sinauer Press. Sunderland, MA.

Galatowitsch SM, Bohnen J. 2021. Long-term recovery of a restored palustrine wetland: the role of monitoring and adaptive management. Wetlands 41: 80. Doi.org/10.1007/s13157-021-01478-7.

Galatowitsch SM, Van der Valk AG. 1996. The vegetation of restored and natural prairie wetlands. Ecological Applications 6: 102-112.

Hall SJ, Zedler JB. 2010. Constraints on sedge meadow self-restoration in urban wetlands. Restoration Ecology 5: 671-680.

Holaday AS, Schwilk DW, Waring EF, Guvvala H, Griffin CM, Lewis OM. 2015. Plasticity of nitrogen allocation in the leaves of the invasive wetland grass, *Phalaris arundinacea* and co-occuring *Carex* species determines the photosynthetic sensitivity to nitrogen availability. Journal of Plant Physiology 177: 20-29.

Kercher S, Zedler JB. 2004. Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. Oecologia 138:455-464.

Kettenring K, Galatowitsch SM. 2007. Tools for *Carex* revegetation in freshwater wetlands: Understanding dormancy loss and germination temperature requirements. Plant Ecology 193:157-169.

Kettenring K, Galatowitsch SM. 2011. Seed rain of restored and natural prairie wetlands. Wetlands 31:283–294. Doi 10.1007/s13157-011-0159-6.

Kost MA, de Steven D. 2000. Plant community responses to prescribed burning in Wisconsin sedge meadows. Natural Areas Journal 20: 36-45.

Larkin D, Bruland G, Zedler JB. 2016. Chapter 10, Heterogeneity theory and ecological restoration. *In:* Palmer M, Zedler JB, Falk D. 2016. Foundations of Restoration Ecology, 2nd Edition. Island Press, Washington, DC.

Larkin D, Lishawa J, Tuchman N. 2012. Appropriation of nitrogen by the invasive Cattail *Typha* x *glauca*. Aquatic Botany 100: 60-66.

Lawrence BA, Zedler JB. 2011. Formation of tussocks in sedges: effects of hydroperiod and nutrients. Ecological Applications 21: 1745-1759.

Lawrence BA, Zedler JB. 2013. Carbon storage by *Carex stricta* tussocks: A restorable ecosystem service? Wetlands 33:483-493.

Lawrence B, Fahey T, Zedler JB. 2013. Root dynamics of *Carex stricta*-dominated tussock meadows. Plant and Soil 364:325-339. Doi. 10.1007/s11104-012-1360-y.

Lemmer M, Rochefort L, Strack M. 2021. Greenhouse gas emissions dynamics in restored fens after in-situ oil sands well pad disturbances of Canadian boreal peatlands. Frontiers in Earth Science. 30 November 2020.| Doi.org/10.3389/feart.2020.557943.

Lehtinen RM, Galatowitsch SM. 2001. Colonization of restored wetlands by amphibians in Minnesota. The American Midland Naturalist 145: 388-396.

Levine JM. 2000. Species diversity and biological invasions: Relating local process to community pattern. Science 288: 852–854.

Marsh GP. 1864. Man and Nature, or Physical Geography as Modified by Human Action. University of Washington Press, Seattle, WA.

MEA. 2005. Millenium Ecosystem Assessment. Ecosystems and Human Well Being: Synthesis. Island Press, Washington DC.

Middleton B. 2002. Nonequilibrium dynamics of sedge meadows grazed by cattle in southern Wisconsin. Plant Ecology 161: 89-110.

Miller N, Kline J, Bernthal T, Wagner J, Smith C, Axler M, Matrise M, Kille M, Silveira M, Moran P, Gallagher Jarosz S, Brown J. 2017. Wetlands by Design: A watershed approach for Wisconsin. Wisconsin Department of Natural Resources and The Nature Conservancy. Madison, WI.

Moreno-Mateos D, Barbier EB, Jones PC, Jones HP, Aronson J, López-López JA, McCrackin ML, Meli P, Montoya D, Rey Benayas JM. 2017. Anthropogenic ecosystem disturbance and the recovery debt. Nature Communications 8: 14163. Doi.10.1038/ncomms14163.

Palmer MA, Zedler JB, Falk D, editors. 2016. Foundations of Restoration Ecology, 2nd Edition. Island Press, Washington DC.

Panci HG, Niemi GJ, Regal RR, Tozer DC. Gehring TM, Howe RW, Norment CJ. 2017. Influence of local, landscape, and regional variables on Sedge and Marsh wren occurrence in Great Lakes Coastal Wetlands. Wetlands 37: 447-459. Doi.10.1007/s13157-017-0881-9.

Rochefort L, LeBlanc M-C, Bérubé V, Hugron S, Boudreau S, Pouliot B. 2016. Reintroduction of fen plant communities on a degraded minerotrophic peatland. Canadian Journal of Botany 94(11): 1041–1051.

Rojas IM, Zedler JB. 2015. An invasive exotic grass reduced sedge meadow species richness by half. Wetlands Ecology and Management 23(4):649-663.

Strassburg BBN. 2021. A decade for restoring earth. Science 374(6564): 125.

Thompson A, Luthin C. 2010. Wetland Restoration Handbook for Wisconsin Landowners, 2nd Edition. Wisconsin Department of Natural Resources. Madison, WI.

Vanausdall RA, Dinsmore SJ. 2020. Detection and density of breeding marsh birds in Iowa wetlands. PLoS ONE 15(1): e0227825. Doi.org/10.1371/journal.pone.0227825

Verdone M, Seidl A. 2017. Time, space, place, and the Bonn Challenge global forest restoration target. Restoration Ecology 25(6):903-911. Doi.org/10.1111/rec.12512.

Watson KB, Ricketts T, Galford G, Polasky S, O'Niel-Dunne J. 2016. Quantifying flood mitigation services: The economic value of Otter Creek wetlands and floodplains to Middlebury, Vermont. Ecological Economics 130: 16–24.

Werner KJ, Zedler JB. 2002. How sedge meadow soils, microtopography, and vegetation respond to sedimentation. Wetlands 22: 451–466.

Whisenant S. 1999. Repairing Damaged Wildlands: A process-oriented landscape-scale approach, Cambridge University Press, Cambridge, England, UK.

Wilcox J, Zedler JB. 2005. Interconnected restoration challenges: Controlling and reestablishing natives. Leaflet 22. Online, Arboretum, University of Wisconsin, Madison, WI.

Wilson SD, Partel M. 2003. Extirpation or coexistence? Management of a persistent introduced grass in a prairie restoration. Restoration Ecology 11: 410–16.

Woo I, Zedler JB. 2002. Can nutrients alone shift a sedge meadow towards the invasive *Typha* x *glauca?* Wetlands 22: 509-521.

Zedler JB. 1966. Buena Vista Marsh in Historical Perspective. MS Thesis, University of Wisconsin, Madison, WI.

Zedler JB. 2010. Tussock sedge—A restoration superplant? Leaflet 22. Online, Arboretum, University of Wisconsin, Madison, WI.

Zedler JB, Kercher S. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes, Critical Reviews in Plant Sciences 23(5): 431-452. Doi.10.1080/07352680490514673.

Chapter 7 • How Can We Grow And Manage Tussock Sedge?

Bilgri A. 2009. N allocation in *Carex stricta* in response to nitrogen and water level treatments. Botany Senior Thesis, Botany Department, University of Wisconsin, Madison, WI.

Budelsky RA, Galatowitsch SM. 1999. Effects of moisture, temperature, and time on seed germination of five wetland *Carices:* Implications for restoration. Restoration Ecology 7: 86–97.

Budelsky RA, Galatowitsch SM. 2004.Establishment of *Carex stricta* Lam. seedlings in experimental wetlands with implications for restoration. Plant Ecology 175: 91–105.

Coladonato M. 1994. Effect of prescribed burning on upright sedge in quaking aspen woodlands in southern Ontario. See *Carex stricta In:* Fire Effects Information system, Online. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. https://www.fs.fed.us/database/feis/.

Gallagher SK. 2009. Use of nitrogen and water treatments to manipulate *Carex stricta* Lam. propagules. MS Thesis, University of Wisconsin, Madison, WI.

Gallagher SK, Zedler JB, with Lawrence B, Bilgri A, Frieswyk C, Kercher S, Hall S, Peach M, Werner K, Woo I. 2010. Tussock sedge—a restoration "superplant"? Leaflet 22. Online, Arboretum. University of Wisconsin, Madison, WI.

He Z, Bentley LP, Holaday AS. 2011. Greater seasonal carbon gain across a broad temperature range contributes to the invasive potential of *Phalaris arundinacea* L. (Poaceae, reed canary grass) over the native sedge, *Carex stricta* LAM. (Cyperaceae). American Journal of Botany 98: 20-30.

Herr-Turoff A, Zedler JB. 2005. Does wet prairie vegetation retain more nitrogen with or without *Phalaris* invasion? Plant and Soil 277: 19-34.

Kettenring K, Galatowitsch SM. 2007. Tools for *Carex* revegetation in freshwater wetlands: Understanding dormancy loss and germination temperature requirements. Plant Ecology 193:157-169.

Lawrence BA, Zedler JB. 2013. Carbon storage by *Carex stricta* tussocks: A restorable ecosystem service? Wetlands 33:483-493.

Lawrence, B. A., and J. B. Zedler. 2011. Formation of tussocks in sedges: Effects of hydroperiod and nutrients. Ecological Applications 21: 1745-1759.

Lindig-Cisneros R, Zedler JB. 2002. *Phalaris arundinacea* L. seedling establishment: Effects of canopy complexity in fen, mesocosm and restoration experiments. Canadian Journal of Botany 80: 617-624.

Prasser N, Zedler JB. 2010. Salt tolerance of invasive *Phalaris arundinacea* exceeds that of native *Carex stricta* (Wisconsin). Ecological Restoration 28: 238-240.

Zedler JB. 2016. Phenology of *Carex stricta:* It pays to be tall! Wetland Science & Practice 33(1): 14-21. https://issuu.com/societyofwetlandscientists/docs/march_2016_wsp.

Zedler JB, Potter K. 2008. Southern Wisconsin's herbaceous wetlands: Their recent history and precarious future. Pages 193-210 in The Vanishing Present. Waller D, Rooney T, Editors. University of Chicago Press, Chicato, IL.

Chapter 8 • Why should we protect all the values of wetlands?

Costello DF. 1936. Tussock meadows in southeastern Wisconsin. Botanical Gazette 97: 610–648.

Davidson NC, van Dam AA, Finlayson CM, McInnes RJ. 2019. Worth of wetlands: Revised global monetary values of coastal and inland wetland ecosystem services. Marine and Freshwater Research 70: 1189-1194.

Zedler JB, Potter K. 2008. Southern Wisconsin's herbaceous wetlands: Their recent history and precarious future. Pages 193-210 in The Vanishing Present. Waller D, Rooney T, Editors. University of Chicago Press, Chicago, IL.

Chapter 9 • Let's protect wetlands for their services and our well-being!

Costanza R, dArge R, de Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S., Oneill, RV, Paruelo J, Raskin RG, Sutton P, van den Belt M. 1997. The value of the world's ecosystem services and natural capital. Nature 387(6630): 253–260.

Costanza R, de Groot R, Braat L, Kubiszewski I, Fioramonti L, Sutton P, Farber S, Grasso M. 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosystem Services 28: 1–16.

Dahl T. 1990. Wetlands losses in the United States 1780s to 1980s. Department of the Interior, US Fish and Wildlife Service, Washington, DC.

Davidson NC, Finlayson CM. 2018. Extent, regional distribution and changes in area of different classes of wetlands. Marine and Freshwater Research 69: 1525–1533.

Davidson NC, Fluet-Chouinard E, Finlayson CM. 2018. Global extent and distribution of wetlands: Trends and issues. Marine and Freshwater Research 69: 620–627.

Gardner R, Okuno E, Tai S, Siobhan Fennessy M, Johnston C, Otte M, Palmer M, Perry J, Simenstad C, Tanner B, Tufford D, Turner RE, Work K, Yaich S, Zedler JB. 2019. Advocating for science: Amici curiae brief of wetland and water scientists in support of the Clean Water Rule. Wetlands 39:403–414. Doi.org/10.1007/s13157-019-01160-z.

Ward ND, Bianchi TS, Martin JB, Quintero J, Sawakuchi HO, Cohen MJ. 2020. Pathways for methane emissions and oxidation that influence the net carbon balance of a subtropical cypress swamp. Frontiers in Earth Science 8:573. Doi.org/10.3389/feart.2020.573357.